A Comparative Study of Some of the Social Communication Patterns of Cormorants and Related Birds in the Pelecaniformes.

by

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A thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy in the Department of Zoology

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The University of British Columbia,
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A COMPARATIVE STUDY OF SOME OF THE SOCIAL
COMMUNICATION PATTERNS OF CORMORANTS
AND RELATED BIRDS IN THE PELECANIFORMES

ABSTRACT

A comparative study was made of the social communication patterns of Pelecanus erythrorhynchos, P. onocrotalus, P. crispus, P. occidentalis, Morus basanus, Sula sula, Anhinga anhinga, Phalacrocorax carbo, Ph. auritus, Ph. olivaceus, Ph. aristotelis, Ph. urile, Ph. pelagicus, Ph. penicillatus, and Fregata magnificens.

It was found that the signal patterns are combinations of a limited number of discrete postures, movements, and sounds, and that they are mainly derivatives from four main sources, locomotion, fighting, nest-building, and begging.

The take-off was found to consist of three phases, look, crouch, and leap. From the look and crouch phases the Sulisoidea have evolved their pre-take off displays, while from the recovery after landing they have evolved their post-landing displays.

The sky-pointing, a male-advertising display of Sula, is a derivative of the pre-take off display of Morus and is the origin of the wing-waving as a male-advertising display in Anhinga and Phalacrocorax.

Threat displays have evolved into recognition displays in the bill-raising of the Pelecanidae, the head-throwing of Sula sula, the gaping of the Phalacrocoracidae, and into the first part of a male-advertising display, the darting, of Phalacrocorax aristotelis.

Nest-indicating displays have evolved from the reaching for nest material into the reach-bowing of Pelecanus erythrorhynchos, and from nest-worrying movements into the wave-bowing of P. erythrorhynchos, the wing-bowing of Morus, the front-bowing of Sula sula, the quiver-bowing of S. leucogaster and S. dactylatra, the snap-bowing of Anhinga anhinga, the front-bowing of Ph. aristotelis and the gape-bowing of Ph. melanoleucus.

The food-begging displays of the chicks have evolved into the pre-landing displays of the Pelecaniformes which in some species also serve as recognition and male-advertising displays on the nest site.

From a comparison of the taxonomic distribution of the form, function and derivation of the social communication patterns in the Pelecaniformes, it was concluded that they reflect the phylogenetic implications of the current systematic classifications of the order.

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Abstract.

A comparative study was made of the social communication patterns of *Pelecanus erythrorhynchos*, *P. onocrotalus*, *P. crispus*, *P. occidentalis*, *Morus bassanus*, *Sula sula*, *Anhinga anhinga*, *Phalacrocorax carbo*, *Ph. auritus*, *Ph. olivaceus*, *Ph. aristotelis*, *Ph. urile*, *Ph. pelagicus*, *Ph. penicillatus*, and *Fregata magnificens*.

It was found that the signal patterns are combinations of a limited number of discrete postures, movements, and sounds, and that they are mainly derivatives from four main sources, locomotion, fighting, nest-building, and begging.

The take-off was found to consist of three phases, look, crouch, and leap. From the look and crouch phases the Suloidea have evolved their pre-take off displays, while from the recovery after landing they have evolved their post-landing displays. The pre-take off and post-landing displays are combined into a hop display in this super-family.

The sky-pointing, a male-advertising display of *Sula*, is a derivative of the pre-take off display of *Morus* and is the origin of the wing-waving as a male-advertising display in *Anhinga* and *Phalacrocorax*. The throw-back which is the second part of the male-advertising display of *Phalacrocorax aristotelis* is a derivative of the wing-waving display of the other cormorants.
Threat displays have evolved into recognition displays in the bill-raising of the Pelecanidae, the head-throwing of Sula sula, the gaping of the Phalacrocoracidae, and into the first part of a male-advertising display, the darting, of Phalacrocorax aristotelis.

Nest-indicating displays have evolved from the reaching for nest-material into the reach-bowing of Pelecanus erythrorhynchos, and from nest-worrying movements into the wave-bowing of P. erythrorhynchos, the wing-bowing of Morus, the front-bowing of Sula sula, the quiver-bowing of S. leucogaster and S. dactylatra, the snap-bowing of Anhinga anhinga, the front-bowing of Ph. aristotelis and the gape-bowing of Ph. melanoleucus.

The food-begging displays of the chicks have evolved into the pre-landing displays of the Pelecaniformes which in some species also serve as recognition and male-advertising displays on the nest site and in the Sulidae, Anhingidae, Phalacrocoracidae, and Fregatidae accompany the transfer of nest-material between members of a pair at the nest site. The food-begging derived displays also include the aerial displays of Pelecanus erythrorhynchos, the head-wagging of the Sulidae, the kink-throating of the Anhingidae and Phalacrocoracidae, the rattling of the Fregatidae, and the aerial displays of the Phaethontidae.

From a comparison of the taxonomic distribution of the form, function and derivation of the social
communication patterns in the Pelecaniformes, it was concluded that they reflect the phylogenetic implications of the current systematic classifications of the order.
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This thesis is dedicated to Apollonius Tyanaeus, who is said to have travelled many kingdoms over to learn the language of beasts and birds.

Cunningham 1866
## Table of Contents

### Introduction

- Object of the study.............................................. 1
- A review of some aspects of animal communication.. 2
- A review of some aspects of the order Pelecaniformes.............................................. 6

### Methods

- Species studied.................................................. 13
- Species names used.......................................... 16
- Observations and recording................................. 18
- Display nomenclature........................................ 23

### Display descriptions

#### Locomotion and its derivatives

- Locomotion..................................................... 25
- Take off.......................................................... 28
- Post-landing.................................................... 42
- Hop................................................................. 51
- Stepping....................................................... 54
- Male-advertising............................................. 56

#### Fighting and its derivatives

- Fighting.......................................................... 71
- Threat............................................................ 74
- Recognition..................................................... 79
- Male-advertising............................................. 98

#### Nest-building and its derivatives

- Nest construction............................................. 101
Defensive nest-indicating......................... 107
Recognition and bowing............................ 108
Begging and its derivatives.
  Food-begging.................................. 132
  Water-begging.................................. 136
  Recognition.................................... 137

Discussion.
  Components of communication patterns......... 166
  Functions of communication patterns.......... 178
  Phylogeny of communication patterns.......... 183
  Phylogeny of the Pelecāniformes.............. 199

Conclusions.................................... 208
Summary......................................... 209
Literature cited.................................. 211
### List of Figures

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Walking and Bill-up-face-away</td>
<td>27</td>
</tr>
<tr>
<td>2</td>
<td>Diagram of Three Phases of Take off</td>
<td>33</td>
</tr>
<tr>
<td>3</td>
<td>Take off of Morus bassanus</td>
<td>34</td>
</tr>
<tr>
<td>4</td>
<td>Pre-take off, M.capensis and M.serrator</td>
<td>35</td>
</tr>
<tr>
<td>5</td>
<td>Pre-take off, S.sula and S.dactylatra</td>
<td>36</td>
</tr>
<tr>
<td>6</td>
<td>Pre-take off, A.anhinga</td>
<td>37</td>
</tr>
<tr>
<td>7</td>
<td>Pre-take off, Ph.carbo, Ph.auritus and Ph.olivaceus</td>
<td>38</td>
</tr>
<tr>
<td>8</td>
<td>Take off and Hop of Ph.aristotelis</td>
<td>39</td>
</tr>
<tr>
<td>9</td>
<td>Pre-take off, Ph.urile, Take off &amp; Hop, Ph.pelagicus</td>
<td>40</td>
</tr>
<tr>
<td>10</td>
<td>Take off and Hop of Ph.penicillatus</td>
<td>41</td>
</tr>
<tr>
<td>11</td>
<td>Neck-grabbing in M.bassanus and M.capensis</td>
<td>46</td>
</tr>
<tr>
<td>12</td>
<td>Post-landing Postures of Sulidae</td>
<td>47</td>
</tr>
<tr>
<td>13</td>
<td>Post-landing Postures of Phalacrocoracidae</td>
<td>48</td>
</tr>
<tr>
<td>14</td>
<td>Post-landing Postures of Phalacrocoracidae</td>
<td>49</td>
</tr>
<tr>
<td>15</td>
<td>Median Crest Postures of Ph.carbo</td>
<td>50</td>
</tr>
<tr>
<td>16</td>
<td>Diagram explaining frequency distributions of tail elevations</td>
<td>58</td>
</tr>
<tr>
<td>17</td>
<td>Sky-pointing of Sulidae</td>
<td>68</td>
</tr>
<tr>
<td>18</td>
<td>Wing-waving and Snap-bowing of A.anhinga</td>
<td>69</td>
</tr>
<tr>
<td>19</td>
<td>Wing-waving of Phalacrocoracidae</td>
<td>70</td>
</tr>
<tr>
<td>20</td>
<td>Fighting of Phaethon aethereus and Morus bassanus</td>
<td>73</td>
</tr>
<tr>
<td>21</td>
<td>Pelecanus erythrorhynchos threatening gull</td>
<td>77</td>
</tr>
<tr>
<td>22</td>
<td>Threat Postures of Pelecaniformes</td>
<td>78</td>
</tr>
<tr>
<td>23</td>
<td>Bill-raising in P.onocrotalus and P.erythrorhynchos</td>
<td>81</td>
</tr>
<tr>
<td>Figure</td>
<td>Description</td>
<td>Page</td>
</tr>
<tr>
<td>--------</td>
<td>-----------------------------------------------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>24</td>
<td>Bill-raising in <em>P. crispus</em></td>
<td>82</td>
</tr>
<tr>
<td>25</td>
<td>Head-throwing, Darting, and Gaping</td>
<td>92</td>
</tr>
<tr>
<td>26</td>
<td>Gaping of <em>Ph. carbo</em> Male and Female</td>
<td>93</td>
</tr>
<tr>
<td>27</td>
<td>Gaping of <em>Ph. auritus</em>, <em>Ph. olivaceus</em>, and <em>Ph. aristotelis</em></td>
<td>94</td>
</tr>
<tr>
<td>28</td>
<td>Pointing of Phalacrocoracidae</td>
<td>97</td>
</tr>
<tr>
<td>29</td>
<td>Pointing and Kink-throating of <em>A. anhinga</em></td>
<td>100</td>
</tr>
<tr>
<td>30</td>
<td>Reach-bowing of <em>P. erythrorhynchos</em> &amp; <em>P. occidentalis</em></td>
<td>111</td>
</tr>
<tr>
<td>31</td>
<td>Bowing</td>
<td>119</td>
</tr>
<tr>
<td>32</td>
<td>Food-begging and Feeding of Chicks</td>
<td>134</td>
</tr>
<tr>
<td>33</td>
<td>Water- and Food-begging &amp; Feeding of Chicks</td>
<td>135</td>
</tr>
<tr>
<td>34</td>
<td>Aerial Pouch Expansion in <em>P. erythrorhynchos</em></td>
<td>140</td>
</tr>
<tr>
<td>35</td>
<td>Head-wagging and Neck-preening</td>
<td>144</td>
</tr>
<tr>
<td>36</td>
<td>Mutual Head-wagging</td>
<td>145</td>
</tr>
<tr>
<td>37</td>
<td>Kink-throating</td>
<td>157</td>
</tr>
<tr>
<td>38</td>
<td>Rattling of <em>Fregata magnificens</em></td>
<td>161</td>
</tr>
<tr>
<td>39</td>
<td>Aerial Display of <em>Phaethon rubricauda</em></td>
<td>164</td>
</tr>
<tr>
<td>40</td>
<td>Aerial Display of <em>Ph. lepturus</em> and <em>Ph. aethereus</em></td>
<td>165</td>
</tr>
<tr>
<td>41</td>
<td>Phylogenetic Tree of Pre-take off Derivatives</td>
<td>187</td>
</tr>
<tr>
<td>42</td>
<td>Phylogenetic Tree of Threat Derivatives</td>
<td>189</td>
</tr>
<tr>
<td>43</td>
<td>Phylogenetic Tree of Nest-building Derivatives</td>
<td>191</td>
</tr>
<tr>
<td>44</td>
<td>Phylogenetic Tree of Food-begging Derivatives</td>
<td>193</td>
</tr>
<tr>
<td>45</td>
<td>Phylogenetic Tree of the Pelecaniformes adapted from Lanham</td>
<td>194</td>
</tr>
<tr>
<td>46</td>
<td>Phylogenetic Tree of the Pelecaniformes adapted from Sibley</td>
<td>195</td>
</tr>
</tbody>
</table>
Figure  Page

47  Common Social Attributes of Pelecaniform Genera... 196
48  Common Social Attributes of Sulid Species......... 197
49  Common Social Attributes of Phalacrocoracid Species................................. 198
### List of Tables

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>64</td>
</tr>
<tr>
<td>2</td>
<td>65</td>
</tr>
<tr>
<td>3</td>
<td>66</td>
</tr>
<tr>
<td>4</td>
<td>67</td>
</tr>
<tr>
<td>5</td>
<td>87</td>
</tr>
<tr>
<td>6</td>
<td>88</td>
</tr>
<tr>
<td>7</td>
<td>89</td>
</tr>
<tr>
<td>8</td>
<td>90</td>
</tr>
<tr>
<td>9</td>
<td>91</td>
</tr>
<tr>
<td>10</td>
<td>96</td>
</tr>
<tr>
<td>11</td>
<td>106</td>
</tr>
<tr>
<td>12</td>
<td>120</td>
</tr>
<tr>
<td>13</td>
<td>121</td>
</tr>
<tr>
<td>14</td>
<td>122</td>
</tr>
<tr>
<td>15</td>
<td>123</td>
</tr>
<tr>
<td>16</td>
<td>124</td>
</tr>
<tr>
<td>17</td>
<td>125</td>
</tr>
<tr>
<td>18</td>
<td>126</td>
</tr>
<tr>
<td>Table</td>
<td>Page</td>
</tr>
<tr>
<td>-------</td>
<td>------</td>
</tr>
<tr>
<td>19 Sequential Chart of <em>Ph. carbo</em> Females on Nest Site, Male present, Naardermeer, Holland</td>
<td>127</td>
</tr>
<tr>
<td>20 Sequential Chart of <em>Ph. auritus</em> Males on Nest Site</td>
<td>128</td>
</tr>
<tr>
<td>21 Sequential Chart of <em>Ph. aristotelis</em> Females on Nest Site, Male present</td>
<td>129</td>
</tr>
<tr>
<td>22 Sequential Chart of <em>Ph. pelagicus</em> Males on Nest Site, Female present</td>
<td>130</td>
</tr>
<tr>
<td>23 Sequential Chart of <em>Ph. pelagicus</em> Males alone on Nest Site</td>
<td>131</td>
</tr>
<tr>
<td>24 Frequency and Duration of Head-wagging</td>
<td>146</td>
</tr>
<tr>
<td>25 Frequency of Tail Elevations during Head-wagging in <em>Morus bassanus</em></td>
<td>147</td>
</tr>
<tr>
<td>26 Frequency of Tail Elevations during Neck-preening in <em>Morus bassanus</em></td>
<td>148</td>
</tr>
<tr>
<td>27 Sequential Chart of <em>M. bassanus</em>, one on Nest Site</td>
<td>149</td>
</tr>
<tr>
<td>28 Sequential Chart of <em>M. bassanus</em>, two on Nest Site</td>
<td>150</td>
</tr>
<tr>
<td>29 Sequential Chart of <em>S. sula</em>, Males alone on Nest Site</td>
<td>153</td>
</tr>
<tr>
<td>30 Sexual Distinctiveness of Cormorant Display Sounds</td>
<td>177</td>
</tr>
</tbody>
</table>
Introduction.

Object of the study.

This study had its beginnings in a comparative study of the behaviour of Phalacrocorax auritus, Ph. pelagicus, and Ph. penicillatus at Mandarte Island, British Columbia (van Tets 1959). At that time several differences and similarities were noted between the social signals of these cormorants and of Ph. carbo (Haverschmidt 1933, Kortlandt 1938, 1940b, 1949, Portielje 1927), Ph. aristotelis (Selous 1901, 1927), Ph. varius (Serventy and White 1943), and Ph. melanoleucus (Harley 1946).

Since then more species of cormorants and other pelecaniform birds have been studied in order to discover the extent of the taxonomic distribution of these signals and their attributes, the clues these communication patterns can offer towards the elucidation of their phylogenetic origin, and the extent to which these clues can help to unravel further the phylogenetic relationships of the species studied.

This study received some of its inspiration from the comparative avian behaviour studies of the Heinroths (1924-1928, 1955, 1958), Lorenz (1941), Moynihan (1956, 1959, 1962), Tinbergen (1959a), and Cullen (1960).

When two or more animals meet and become aware of each other, there is some transfer of information between them. The more explicit this information is, the less likely it will be that energy is wasted in the form of either inappropriate responses or conflict, as a result of misunderstandings. The amount and form in which a message is transferred is limited by the sensitivity of the sense organs and central nervous system of the recipient and the morphology and behaviour of the sender.

Thus the external appearance of many animals can transmit to those that can perceive it, information as to its specificity, sex, age, and reproductive condition (Udvardy 1957). This is frequently supplemented by an emission of odours, call notes, and electricity, and a display of postures and movements. These signals may help to lure prey, to baffle predators, to intimidate rivals, to warn conspecifics, and to attract the attention of mates, offspring, and flock members. The signals may also help to space animals in their environment (Wynne-Edwards 1962).

How much of the potential information content is actually received, comprehended, and reacted upon can only be determined with models (Tinbergen 1946, 1948, 1954), or by altering the appearance of an animal (Noble 1936).

When animals live together in close proximity as in flocks and colonies, the interactions between them are exceedingly frequent and there is then a strong selective
advantage to increase the amount and specificity of the information that is passed between them, and to increase the predictability of their actions (Marler 1961). Thus it is hardly surprising that the most complex instructions transmitted by animals have been discovered in the hive of the honeybee (von Frisch 1950). Similarly, conventions such as peck orders which are based on individual recognition tend to develop in barnyard and other crowded situations (Allee 1958, Schjelderup-Ebbe 1922, Slijper 1959).

Many of the sea- and water-birds have developed complex displays which may act as signal systems which help them to reproduce successfully in aggregations. There are many advantages to nesting in a colony. A common front of beaks can be presented towards a predator. Full use can be made of a safe and suitable habitat that may be limited in extent such as isolated stacks, islets, sandbars, cliffs, and trees. The reproductive success may be enhanced by the stimulating and synchronizing effects of social facilitation (Coulsen and White 1960).

However, disturbances, misunderstandings, and conflicts in a crowded colony often lead to enormous losses of nests, eggs, and chicks (Abbott 1861, Stonehouse 1960, Vesey-Fitzgerald 1954, 1957). Thus, a panic flight of murres can cause a shower of eggs to roll down a cliff (Kartaschew 1960, Uspenski 1958). A riot in a tree-nesting cormorant colony may cause eggs and chicks to be kicked out of their nests, and the nests themselves to collapse under the weight of the
contestants (Kortlandt 1942, 1949).

Due to the nests being exposed and present in large numbers, a nest that is left unguarded does not survive in most colonies (Beck 1904, Fisher 1906, Kortlandt 1949, McLachlan and Liversidge 1957, Murphy 1936, Perry 1948, Worcester 1911a). At Mandarte Island in British Columbia, eggs are removed by crows and gulls from Double-crested and Pelagic Cormorant nests within five minutes of their being vacated (Drent and Guiguet 1961, van Tets 1959). Later other birds will move in to either claim the nest site or to remove its nest material. Consequently those birds which do not conceal their nests in burrows and vegetation, mount a continual guard over their nest from its definitive start to the time that the chicks are strong enough to defend themselves. This necessitates that the communicatory repertoire of these birds must include signals which facilitate nest relief and nest defence.

Because space is at a premium in most colonies conventions are established with respect to territorial boundaries, landing and perching "rights" near the nest, and communal loafing areas or clubs (Kartaschew 1960, Tinbergen 1952b). These conventions require some transfer of information in order to be effective.

It is not surprising, therefore, that the social behaviour of such colonially nesting birds as penguins, albatrosses, cormorants, herons, gulls, and terns has yielded such a wealth of data and promises to yield much more
A Review of some Aspects of the Order Pelecaniformes.

The order Pelecaniformes consists of six extant families: the Pelecanidae (7 species), the Sulidae (9 species), the Anhingidae (2 species), the Phalacrocoracidae (28 species), the Fregatidae (5 species), and the Phaethontidae (3 species).

The order is characterised by the feet being totipalmate with the web not only supported by the front three digits but also by the hind digit. In their external morphology the families have diverged in the shape and size of the head, neck and tail.

The upper mandible has a terminal hook in the Pelecanidae, Phalacrocoracidae, and Fregatidae, while the Sulidae, Anhingidae and Phaethontidae lack this hook. The external nares are closed in the Sulidae and Phalacrocoracidae (Ewart 1881), reduced in size in the Pelecanidae, Anhingidae, and Fregatidae, and open in the Phaethontidae (Stresemann 1927-1934). Secondary external nares are present in the Sulidae (Ewart 1881, MacDonald 1960). The bill and gular pouch are very large in the Pelecanidae. In the males of the Fregatidae a "gular sac" (Murphy 1936) is inflated like a ballon during courtship (fig. 38). In all the Pelecaniformes, except the Phaethontidae (Howell and Bartholomew 1962), the gular region lacks feathers and is very colourful during the breeding season. Nuptial crests occur in the Pelecanidae, Anhingidae and Phalacrocoracidae.

The Pelecanidae, Phalacrocoracidae, and Anhingidae have relative long necks, while the necks of the Sulidae,
Fregatidae, and Phaethontidae are short. There is a special hinge mechanism at the 8th and 9th cervical vertebrae in the Anhingidae (Garrod 1876, Stresemann 1927-1934). Similar but less specialized modifications of the cervical vertebrae are also present in the Pelecanidae, Sulidae and Phalacrocoracidae, but not the Fregatidae and Phaethontidae (Lanham 1947).

The legs are relatively short and stout throughout the order and very much reduced in size in the Fregatidae and Phaethontidae. The wings are long and adapted for gliding in the Pelecaniformes, except in the Flightless Cormorant, Phalacrocorax harrisi, which has vestigial wings (Gadow 1902, Kuroda 1961, Rothschild 1898).

Each family has a distinctive tail shape. The tail is short and rounded in the Pelecanidae, long and wedge-shaped in the Sulidae, very long, graduated, and with transverse fluting in the Anhingidae, long and rounded in the Phalacrocoracidae, long and deeply forked in the Fregatidae, and long, wedge-shaped, and with extremely elongated and narrow middle two rectrices in the Phaethontidae (Van Tyne and Berger 1959).

The Pelecaniformes have diverged mainly in their fishing and nesting habits. All of them are ichthyophagous, although other more or less "fish-like" aquatic animals, such as newts, squids, and shrimps, are also caught and eaten (Bó 1956, Falla and Stokell 1945, Ferry 1910, Fisher 1904b, Gibson-Hill 1947, Gross 1912, Lowe 1909, McKeown 1944, Palmer 1962, Preble and McAtee 1923, Rand 1959,
Pelicans in captivity kill and eat small birds (Meinertzhagen 1954, 1959) and small mammals (Griffith et al 1829), while frigatebirds at disturbed bird colonies will feed on nestlings, including those of their own species (Beard 1939, Buddle 1938, Stonehouse 1960).

In order to secure their prey the Phaethontidae, the Sulidae, and the Brown Pelican (*Pelecanus occidentalis*) plunge-dive (Tinbergen 1954) like terns from a height down into the water. *P. erythrorhynchos* and *P. crispus* have been seen to dive also on very rare occasions (Hall 1925, Meinertzhagen 1954, 1959).

All the Pelecanidae use their huge lower jaw and gular pouch as a "dipnet" to scoop up fish in shallow water. Sometimes they snatch fish from surfacing cormorants (Forbes 1914, MacGillivray 1923).

The Fregatidae remain on the wing as they pursue the flying fishes, pick food off the surface of the sea, snatch nestlings from their nests, and molest other seabirds in order to get their food. They also drink (Bailey 1956, Fisher 1904a, 1906, Lowe 1909) and bathe (Bonhote 1903) on the wing. Occasionally Red-footed Boobies, *Sula sula*, also catch flying fishes on the wing (Gifford 1913).

The Anhingidae and the Phalacrocoracidae dive from the water surface and swim under water. Whereas the Anhingidae stalk and spear their prey (Gurney 1887, Serventy
1939b), the Phalacrocoracidae search out and grab their food. Like herons above water, anhingas spread their wings under water and thus lure fish in towards the shadow so created (Allen 1961, Forbush 1922, Palmer 1962).

Various degrees of cooperative and communal fishing occur in the Pelecanidae and the Phalacrocoracidae. Enormous numbers of pelecaniform as well as other seabirds may gather to feed on a surfacing fish school (Bartholomew 1942, Goss 1888a, Meinertzhagen 1954, 1959, Murphy 1924, 1936, Nelson 1903, Oliver 1955, Sefton 1927, Serventy 1939a, Taverner 1934, Ticehurst and Cheesman 1925, van Tets 1959).

Within each family there is a great diversity in the types of nest sites that are used. The Phaethontidae nest in cavities which may be either in rock, soil, or trees, or sheltered underneath shrubbery. The other five families nest more or less out in the open either in trees, in bushes, on flat ground, or against cliff sides on rock ledges.

All the Pelecaniformes have nidicolous young and except for the Phaethontidae they are naked when they hatch.

Like most other birds the Pelecaniformes help to thermoregulate their eggs and chicks by brooding them when it is cold, and shading them when it is hot (Bartholomew et al 1953, Bartholomew and Dawson 1954). In addition to this some cormorant species, Phalacrocorax carbo and Ph. auritus, pour water down the throats of their nestlings during warm weather (Kortlandt 1949, Palmer 1962, Schuster 1935, van Dobben 1952, van Tets 1959). Ph. pelagicus cools
its nest content by bringing in wet grass and algae. *Pelecanus erythrorhynchos* cools its eggs and young by sprinkling water from its body plumage over them (Murbarger 1956, Walker 1943).

Most, if not all, pelecaniform birds have a basic courtship sequence in common, which serves to establish the nest-bond and the pair-bond for one season if not more. It consists of the male selecting the nest site, and the female selecting a male that is advertising for a female on his nest site. When a male accepts the advances of a female, he will eventually surrender the nest site to her, and leave to fetch nest material to present to her. She will then alone, or assisted by the male, weave and secure this material into a nest structure. Copulation normally occurs on the nest site, usually in between several bouts of nest material-fetching by the male. Reverse mounting often follows the arrival of the female at the nest, but normally no cloacal contact is made. There are no special pre- and post-coital displays in the Pelecaniformes, as there are in some other avian orders, such as the Anseriformes (Lorenz 1941). On the nest site the pair bond is strengthened by such joint endeavours as nest-building, allo-preening (Cullen 1953), and nest-defence.

Both sexes often "circle-fly" one at a time away from the nest and back again during the courting period. This probably helps the birds to get fully familiar with the location of the nest and its approaches (Kortlandt 1949).
Some of the reports of cormorant games and courtship displays on the water (Jewett et al 1953, Mendall 1936a), are good descriptions of their spectacular method of bathing.

After the pair-bond has been established, both birds take turns at guarding the nest, incubating the eggs, and caring for the nestlings. During the incubation period the sexual differences start to wane, and the female will also bring in nest material.

During the non-reproductive season and especially just before and just after the nesting season, several uncoordinated forms of courtship may be seen (Bartholomew 1943, Kortlandt 1940b, 1942, 1949, 1959, Mendall 1936b, Metcalfe 1950, Perry 1948, Serventy and White 1943, Sprunt 1951, Warham 1958). For example, a male may follow one or more females around and will use several temporary "nest sites" for display purposes in close proximity to them. This may occur almost anywhere, at the "club", at "haul out" spots near the fishing area, and even on the water and in the air. Sometimes a mated male can be seen, while his female is guarding their nest and its contents, courting and even mounting other females at the club.

Although the individual display patterns retain their species-specificity during the uncoordinated courtship bouts they do not lead directly to the formation of the pair- and nest-bonds which are essential for the reproduction of the species.

Due to the prominence of the nest in the
courtship of these birds, they are not only sexually but also positionally diethic, for the behaviour of the "in" or "sitting" bird differs markedly, irrespective of sex, from that of the "out" or "standing" bird (Kortlandt 1949).

Failure to recognize the existence of uncoordinated courtship, positional diethism, and, in mated birds, diminishing secondary sexual differences, has led to many erroneous interpretations of field observations. Thus sitting cormorant males were assumed to be females by Davis and Friedmann (1936), Haverschmidt (1933), Michael (1935), Murphy (1924), Portielje (1927), Snodgrass and Heller (1903), until Lewis (1929) shot a male advertising on his nest (Witherby et al 1943).
Methods.

Species studied.

The following species were studied at the locations and dates listed below:

American White Pelican, *Pelecanus erythrorhynchos*,
Stum Lake, British Columbia, Canada,
24 May - 2 June 1960.
Mississippi delta, Louisiana, U.S.A.
13 January 1961.

Eastern White Pelican, *Pelecanus onocrotalus*,
Amsterdam Zoological Gardens, Amsterdam, Holland,
at intervals June 1961 - May 1962.

Dalmatian Pelican, *Pelecanus crispus*,
Amsterdam Zoological Gardens, Amsterdam, Holland,
at intervals June 1961 - May 1962.

Brown Pelican, *Pelecanus occidentalis*,
Belize and Half Moon Caye, British Honduras,
North Island, Mississippi delta, Louisiana, U.S.A.,
13 January and 20 - 21 May 1961.

Northern Gannet, *Morus bassanus*,
Bonaventure Island, Quebec, Canada,
23 June - 7 July 1960.

Red-footed Booby, *Sula sula*,
Half Moon Caye, British Honduras,
Anhinga, *Anhinga anhinga*,
Avery Island, Louisiana, U.S.A.,

Great Cormorant, *Phalacrocorax carbo*,
Cape Tryon, Prince Edward Island, Canada, 11 July 1960,
East Point, " " " " , 13 July 1960,
Crystal Cliff, Nova Scotia, Canada, 15 July 1960,
Cheticamp Island, " " " " , 19 July 1960,
Amsterdam Zoological Gardens, Amsterdam, Holland,
at intervals June 1961 - May 1962.
Naardermeer, Holland, 9 February - 22 March 1962,
Rotterdam Zoological Gardens, Rotterdam, Holland,
28 March 1962.

Double-crested Cormorant, *Phalacrocorax auritus*,
Mandarte Island, British Columbia, Canada,
3 May - 4 September 1957, 1 May - 23 August 1958,
27 April - 14 September 1959, 2-6 May 4-7 August 1960,
3-4, 12-13 June, 12-13 July, 1-2 September 1962,
Perce Rock and Bonaventure Island, Quebec, Canada,
23 June - 7 July 1960,
Cape Tryon, Prince Edward Island, Canada, 11 July 1960,
Lacassine National Wildlife Refuge, Louisiana, U.S.A.,
Amsterdam Zoological Gardens, Amsterdam, Holland,
at intervals June 1961 - May 1962.
Olivaceous Cormorant, *Phalacrocorax olivaceus*,
Lacassine National Wildlife Refuge, Louisiana, U.S.A.,

Shag, *Phalacrocorax aristotelis*,

Red-faced Cormorant, *Phalacrocorax urile*,
Attu Island, Alaska, U.S.A., 8 - 10 June 1960,

Pelagic Cormorant, *Phalacrocorax pelagicus*,
Mandarte Island, British Columbia, Canada,
3 May - 4 September 1957, 1 May - 23 August 1958,
27 April - 14 September 1959, 2-6 May, 4-7 August 1960,
3-4, 12-13 June, 12-13 July, 1-2 September 1962,
Attu Island, Alaska, U.S.A., 8 - 10 June 1960,

Brandt Cormorant, *Phalacrocorax penicillatus*,
Mandarte Island, British Columbia, Canada,
3 May - 4 September 1957, 1 May - 23 August 1958,
27 April - 14 September 1959, 2-6 May, 4-7 August 1960,
3-4, 12-13 June, 12-13 July, 1-2 September 1962.

Magnificent Frigatebird, *Fregata magnificens*,
Belize and Half Moon Caye, British Honduras,
Species names used.

The following list of names which are used in this paper for the living species of the order **Pelecaniformes** is based on the A.O.U. Checklist of 1957, Alexander (1955), Jorgensen (1958), Murphy (1936), Peters (1931), Peterson, et al (1954), and von Boetticher (1957).

### Pelecanidae - Pelicans

<table>
<thead>
<tr>
<th>American White Pelican</th>
<th>Pelecanus erythrorhynchos</th>
<th>Gmelin</th>
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<tbody>
<tr>
<td>Eastern</td>
<td></td>
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<tr>
<td>Pink-backed</td>
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<tr>
<td>Dalmatian</td>
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<tr>
<td>Australian</td>
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<tr>
<td>Grey</td>
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<tr>
<td>Brown</td>
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</table>

### Sulidae - Gannets and Boobies

<table>
<thead>
<tr>
<th>Northern Gannet</th>
<th>Morus bassanus</th>
<th>(Linnaeus)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cape</td>
<td>M. capensis</td>
<td>(Lichtenstein)</td>
</tr>
<tr>
<td>Australian</td>
<td>M. serrator</td>
<td>(G.R.Gray)</td>
</tr>
</tbody>
</table>

| Red-footed Booby        | Sula sula     | (Linnaeus) |
| Masked                  | S. dactylatra | Lesson     |
| Brown                   | S. leucogaster| Boddaert   |
| Abbott's                | S. abbotti    | Ridgway    |
| Blue-footed             | S. nebouxii   | Milne-Edwards |
| Peruvian                | S. variegata  | Tschudi    |

### Anhingidae - Anhingas and Darters

| Anhinga                | Anhinga anhinga | (Linnaeus) |
| Darter                 | A. rufa        | (Daudin)   |

### Phalacrocoracidae - Cormorants

| Great Cormorant         | Phalacrocorax carbo | (Linnaeus) |
| Japanese                | Ph. capillatus     | (Temminck & Schlegel) |
| Cape                    | Ph. capensis      | (Sparman)  |
| Indian                  | Ph. fusciollis    | Stephens   |
| Little Black            | Ph. sulcirostris  | (Brandt)   |
| Pied                    | Ph. varius        | (Gmelin)   |
| Double-crested          | Ph. auritus       | (Lesson)   |
| Olivaceous              | Ph. olivaceus     | (Humboldt) |
- 17 -

Flightless Cormorant
Reed    " Ph. harrisi Rothschild
Pigmy   " Ph. africanus (Gmelin)
Javanese " Ph. phygmaeus (Pallas)
Little Pied " Ph. niger (Vieillot)
Spotted  " Ph. melanoleucus (Vieillot)
Chatham  " Ph. punctatus (Sparman)
Shag     " Ph. featherstoni Buller
Red-faced Cormorant
Pelagic  " Ph. aristotelis (Linnaeus)
Red-legged  " Ph. urile (Gmelin)
Magellan  " Ph. pelagicus Pallas
Bank     " Ph. gaimardi (Lesson)
White-breasted " Ph. magellanicaus (Gmelin)
Guanay   " Ph. neglectus (Wahlberg)
Blue-eyed " Ph. fuscescens (Vieillot)
King     " Ph. bougainvillei (Lesson)
Rough-faced " Ph. atriceps King
Brandt's  " Ph. albiventer (Lesson)
Socotra  " Ph. nigrogularis Ogilvie-Grant & Forbes

Fregatidae - Frigatebirds
Magnificent Frigatebird  Fregata magnificens Mathews
Great     " F. minor (Gmelin)
Ascension " F. aquila Linnaeus
Christmas " F. andrewsi Mathews
Lesser    " F. ariel (G.R. Gray)

Phaethontidae - Tropicbirds
Red-billed Tropicbird  Phaethon aethereus Linnaeus
White-tailed       " Ph. lepturus Daudin
Red-tailed        " Ph. rubricauda Boddart
Observation and recording.

The various study locations differ in how close the birds can be approached without disturbing them. Where it was permitted and possible, wooden blinds were built 20 to 60 feet from the nests. A tent blind was used at the Farne Islands to study the Great Cormorant.

Northern Gannets, Red-footed Boobies, Shags, and Magnificent Frigatebirds tolerated an observer in full view 20 to 30 feet from the nest without a blind. With and without a blind a period of habituation is needed before the birds start to "ignore" the observer.

A 20x to 60x telescope was used to study birds that were more than 30 feet away from the observer.

Individual recognition of the study animals is one of the first requirements for a behaviour study. The disturbance inherent in the current methods of marking birds at a colony, can, in the early stages of the reproductive cycle, frequently cause nest desertion at the very time the courtship displays are most pronounced. This study has therefore benefited a great deal from the banding of nestlings two or more years previous to the time of study. Often the band numbers could be read with the aid of the telescope, and thus a bird of known age and origin could be followed around from one location to another in the colony.

Sometimes a band is wrapped around the leg in such an unusual manner that the bird can be recognized even when the band number is illegible. Such accidental marks
as the several strands of nylon leader that had become attached around the neck of one Double-crested Cormorant, and holes in the webs of the feet, helped to identify birds over a long period of time. Partial albinism consisting of several white wing feathers made it possible to recognize an already banded female Shag in the air as well as on the ground.

Cormorants, as was noticed and used by Kortlandt (1938, 1949) when he studied the Great Cormorant, vary individually in the colouration of the skin and feathers of the head and neck region. Some species, like the Double-crested Cormorant at Mandarte Island, B.C., differ in the shape, size and colour of the nuptial crests. Similarly both sexes of the American White Pelican may have either white or black nuptial crests, and vary in the shape and number of the deciduous nuptial horns on their bills. Forbes (1914) noticed much variation in the facial colouration of the Brown Pelican. These diversifications help to distinguish the various birds associated with a particular nest site.

Most of the recording was done using a notebook. The stereotyped behaviour patterns which were observed to occur repeatedly are referred to provisionally by hieroglyphic symbols in the field notes. This postpones until later the assigning of names to these behaviour patterns, and saves writing time. A record was kept of the properties of these patterns and the situations in which
they occur. Whenever possible comparisons were made with similar movements in other species, and the behaviour of other species in similar situations.

Fortunately for comparative purposes, more than one species of cormorant could be seen courting at the same time in most colonies. For further comparison usually several species of herons, gulls, and alcids were also available. These comparisons helped to point out differences and similarities. They also called attention to some behaviour patterns obvious in some species, but not in others.

Whenever possible still and motion photography was used to record the behaviour patterns. In addition, sketches and diagrams were made in the field. Due to technical and financial limitations no tape recordings were made of the calls emitted during the displays, but as an improvisation the calls were noted down phonetically.

The duration of the displays and the frequency of repetitive displays were measured with the aid of either 16 mm. black and white film at 24 frames per second (f.p.s.), or 8 mm. colour film at 16 f.p.s., or with either a wrist watch or a stop watch and a hand counter. The speeds of the repetitive displays are expressed as cycles per second, where a cycle includes both parts of an alternating movement.

The photographs and the film were used to calculate the frequency distribution of tail elevations during the displays. The tail elevations are grouped in nine 30 degree sectors in the median plane, ranging from vertically
downwards to horizontally forwards (fig. 16 and tables 1-3, 6-10, 12-15, 25, 26).

The film was also used to construct the sequential charts which record how often one display was followed by another. (tables 17-24, 27-29)

Unless otherwise acknowledged the figures have been drawn from photographs, film, and sketches which were made during the course of this study.

Of the pelecaniform species studied only the anhingas and the frigatebirds are sexually dimorphic in their external features. The American White Pelican males were visibly larger than the females. Sexual diethisms were used to determine the sexes of the other species, and the sexual distinctiveness of their displays. Signals were called bisexual if they were done by both members of a pair.

The telescope was used to observe seminal fluid ejaculation and egg-laying. These primary sexual acts are not as frequent as other sexually distinct behaviour patterns, and at some nests due to the angle of observation cannot be observed. Consequently for many birds and some displays sex was deduced secondarily from the sexual distinctiveness of the acts—the sex of which had been determined directly from the primary sexual acts. The assumption was also made that pairs in wild populations are normally heterosexual, and hence the sex of an attribute was crossed-checked by making a record of the behaviour
patterns and courting partners of individually recognizable birds. Homosexual pairs of captive cormorants in flocks with an unbalanced sex ratio, however, have been observed at the Amsterdam Zoological Gardens by Kortlandt (unpublished MS).

At some colonies birds can be autopsied after their behaviour patterns have been recorded, as was done by Courtenay-Latimer (1954), Lewis (1929), and Kortlandt (unpublished MS). One Great Cormorant (*Phalacrocorax carbo*) at the Amsterdam Zoological Gardens which over a period of several years showed both masculine and feminine behaviour patterns was on autopsy found to have both a testis and an ovary (Kortlandt, unpublished MS).

Autopsy was not feasible at the colonies covered in this study. At most colonies the collecting of birds is not permitted by the owners and local authorities. At other colonies collecting is not possible without disturbing the remaining birds and thus preventing further behaviour studies.
Display nomenclature.

The displays that are used by animals during social interactions often resemble to a greater or lesser extent other acts of these animals, which then appear to be out of context (Kortlandt 1940a, 1940c, Tinbergen 1939, 1940). Several explanatory names have been given to various types of such displays which include intention (Daanje 1950, Heinroth 1911) symbolic (Tinbergen 1939), and displacement movements (Kortlandt 1940a, 1940c, Tinbergen 1939, 1951). These terms and their many synonyms are based on the observation that a gradual gradation in function and form can be found in phylogenetically related species between such acts as locomotion, fighting, nest-building, food-begging, and the ritualised social signals that are used between the members of a flock, pair or family. Thus one behaviour pattern can be regarded as a derivative from one or more other behaviour patterns as is outlined in Tinbergen (1952a). In the descriptive part of this study the displays have been arranged according to and are compared with their most probable main derivation.

Functionally the social signals of the "in" bird have been divided in this study into threat, recognition, and male advertising displays. Threatening tends to frighten other animals away, while recognition displays have the opposite effect. Threat signals are used to maintain the individual distance (Hediger 1955), while recognition signals serve to break it down. Recognition
displays are used between members of a pair, between parents and offspring, and sometimes in dense nesting colonies between neighbouring pairs. Male advertising displays occur normally only during the pre-egg stage (sensu Richdale 1950) in males when they are alone on the nest, and do not occur when a female is also present at the nest. Presumably the male advertising displays serve to attract females towards single males, and a mated female towards her nest and mate when the nest lacks eggs. Some of the sexually diethic recognition displays may also have a male advertising function. See discussion - function of communication patterns.

In this study descriptive names have been given to the displays. There is, however, a limit to the number of distinctive postures and movements a bird can use for communication. Hence phylogenetically unrelated displays may look the same in either the same or in different species. Therefore, where the displays of two or more taxa have the same name no homology is implied unless it is specifically stated in the text.

An attempt has been made to use, wherever possible, the same names as have been used by earlier authors for the same displays in the same species. For those displays that have been given several names in the literature these names are mentioned in the descriptive part of this paper.
Display descriptions.
Locomotion and its derivatives.
Locomotion.

On land the Pelecanidae, Sulidae, Anhingidae, and Phalacrocoracidae walk with a high stepping gait or waddle (fig. 1) during which the pelicans frequently spread their wings fully and the anhingas spread them partially for balance. As they move from rock to rock and from perch to perch they often hop with both feet together.

The legs of the Fregatidae and the Phaethontidae are too short for regular walking and they use their wings to aid them in their limited movements on land.

In the water the webbed feet of the Pelecaniformes are used alternately for propulsion while swimming on the surface, and simultaneously to assist the wings during take off. In the Anhingidae and Phalacrocoracidae they are used simultaneously while swimming under water.

The flight of the Pelecaniformes is characterized by the alternation of a number of wing beats with a glide. The pelicans, gannets, boobies, and cormorants often fly grouped in long lines and "V"s, each bird in this manner taking advantage of the vortex caused by the bird ahead (Storer 1948). While the pelicans, anhingas, and frigate-birds are well know for their soaring abilities, the other pelecaniform species will also frequently soar in the air waves that are formed by the cliffs and trees of their nesting colonies (Barlee 1957).
The arrival and departure from the nest sites is often a modification of the usual methods of locomotion as will be outlined in the subsequent sections.
Fig. 1. Walking Pelecanus crispus (top), Phalacrocorax penicillatus with nest material (middle left), Morus bassanus with nest material (middle right), Sula leucogaster with bill-up-face-away (bottom left). Bottom two figures redrawn from Dorward (1962), others from photographs.
Take off.

The take-off for either a flight or a hop can be considered to consist of three phases: look, crouch, and leap (figs. 2 and 3). During the look phase the bird increases its field of vision by raising its head. During the crouch phase the body and sometimes also the head is lowered, thus bringing down the center of gravity in preparation for the leap. During the leap the bird suddenly stretches forwards and upwards, and the resultant momentum helps it to become airborne.

The coiled spring-like mechanism of the crouch and leap phases was recognized and described by Daanje (1950), who like Heinroth (1911) noticed that the crouch phase is often slowed down for display purposes. Heinroth (1911) coined the term "Intentionsbewegungen" (intention movements) for the delayed crouch phases in the display take off in the Anseriformes (Davies 1963, Lorenz 1941), which seem to indicate the intention to depart.

Daanje (1950) tried to show how most of the more spectacular avian courtship displays known at that time could be explained as modified pre-take off postures and movements. He appears, however, to have been unaware of the look phase, and consequently has equated the first phase of the stretch display of the Gray Heron, Ardea cinerea, (Verwey 1930) with the leap phase (Daanje's second phase), and the second phase of the stretch display with the crouch phase (Daanje's first phase). This reversal of phases has
puzzled Baerends and van der Cingel (1962). This problem can be solved by regarding the first phase of the stretch display as a derivative of the look phase rather than the leap phase.

The Sulidae, Anhingidae and Phalacrocoracidae often prolong the look and crouch phases before leaving the vicinity of their nest sites. These pre-take off displays which are described in detail below, probably help to signal their impending departure to their mates and neighbours. Often they step around in the pre-take off posture until they reach a favourable spot and direction for their take off.

No pre-take off displays have been discovered in the Pelecanidae, Fregatidae, and Phaethontidae. This may be due to a lack of observational data.
Gannets

Prior to taking off, the gannets, *Morus bassanus*, *M. capensis*, and *M. serrator*, extend their necks and their bills vertically upwards. The location of the eyes is such that they retain a bifocal vision forward. *M. bassanus*, and *M. serrator* raise their wings upwards with the primaries folded behind the secondaries (figs. 3 & 4) (Cunningham 1866, Perry 1948, 1951, Stresemann 1953, Warham 1958). According to Broekhuysen and Rudebeck (1951) and Gibson-Hill (1948) the wings are spread fully outwards at about 30° to the horizontal in *M. capensis* (fig. 4). In their respective pre-take off postures the gannets step around until a favourable take off position is reached (Gibson-Hill 1948, Perry 1948, 1951, and Warham 1958). During the actual take off *M. bassanus* and *M. serrator* (Warham 1958) spread their wings in a manner similar to the pre-take off posture of *M. capensis* (figs. 3 & 4).

Boobies

The boobies *Sula sula*, *S. dactylatra*, and *S. leucogaster* (Dorward 1962) in their pre-take off posture raise their heads, point their bills forward and slightly
Anhingas

The Anhinga, A.anhinga, points its bill in the direction it intends to take off in, and spreads its wings partially outwards, without the wing tips being raised (fig. 6).

Cormorants

The cormorants vary a great deal in their pre-take off posture. Phalacrocorax carbo, Ph.auritus, Ph.olivaceus, expand their heads and necks as well as raising them, and point their bills forward and slightly upwards. (fig. 7). In addition Ph.olivaceus and Ph.carbo have their median crests up, and Ph.auritus raises its scapulars. Ph.varius bulges its gular pouch and raises its head and neck feathers (Serventy and White 1943). Ph.aristotelis and Ph.penicillatus raise, but do not expand, their heads and necks (figs. 8 & 10). Ph.aristotelis lowers its front crest slightly. Ph.pelagicus and Ph.urile which normally perch facing a cliff frequently take off from the cliff ledges without first pointing their feet in the take off direction (fig. 9). Instead they twist their head, neck, and body
out towards the sea, while their feet remain in place pointing towards the cliff or nestbowl. This is one of the behavioural adaptations which allows these two species to nest and perch on very narrow cliff ledges. On rare occasions they take off from a sea-facing posture. Then their take off is similar to that of other cormorants. Preceding take off the Ph. pelagicus points its wide open bill, and Ph. urile its closed bill in the take off direction.

Some species, Morus capensis (Gibson-Hill 1948), M. serrator (Warham 1958), Phalacrorax carbo, Ph. aristotelis, Ph. auritus, and Ph. pelagicus, utter a characteristic call note prior to the actual take off. After the bird has become airborne a single call note is often emitted by M. bassanus (Cunningham 1866, Perry 1948, 1951), Ph. auritus, and Ph. olivaceus, and a repetitive call note by M. serrator (Warham 1958), Ph. urile, Ph. pelagicus (van Tets 1959), and Ph. gaimardi (Coker 1920). Forbes (1914) reports that Pelecanus occidentalis takes off with a characteristic call note.
Fig. 2. Diagrams of the three phases of the take off, from left to right: look, crouch and leap. The second and third phases have been redrawn from Daanje (1950) with eyes added.
Fig. 3. Successive phases of the take off of *Morus bassanusa*, from left to right: look, crouch and leap. Drawn from photographs.
Fig. 4. Pre-take off posture of *Morus capensis* (top), walking posture of *Morus capensis* (middle), pre-take off posture of *Morus serrator* (bottom). Top and middle figures drawn from photographs in Gibson-Hill (1948), bottom figure drawn from photograph in Warham (1958).
Fig. 5. Pre-take off posture of *Sula dactylatra*, redrawn from Dorward (1962) (top), pre-take off (left bottom) and post take off (right bottom) postures of *Sula sula*, drawn from photographs.
Fig. 6. Pre-take off (left top and bottom) and post-take off (right) postures of *Anhinga anhinga*. Drawn from photographs.
Fig. 7. Successive postures from look to crouch in the pre-take off of *Phalacrocorax carbo* (top three), look phases of the pre-take off of *Ph.auritus* (bottom left), and *Ph.olivaceus* (bottom right). Drawn from photographs, except for bottom right which is redrawn from field sketch.
Fig. 8. *Phalacrocorax aristotelis*, pre-hop (top left), mid hop with post hop display (top right), mid hop without post hop display (middle), pre-take off (bottom left), leap of take off (bottom right). Drawn from photographs.
Fig. 9. *Phalacrocorax pelagicus*, pre-hop (top left), mid hop (top right), pre-take off (middle left and right), leap of take off (bottom right).

*Phalacrocorax urile*, pre-take off (bottom left).

Drawn from photographs.
Fig. 10. *Phalacrocorax penicillatus*, pre-hop (top left), mid hop with post hop display (top right), pre-take off (bottom left), leap of take off (bottom right). Drawn from photographs.
Post-landing.

Immediately after gannets, boobies, anhingas, and cormorants land near conspecifics they frequently display a recovery movement which ends in a taxon specific posture. This posture resembles the pre-take off posture in that the anterior part of the body is held high, and in that the head and neck form a characteristic configuration. A similar post-landing display occurs in the Black-crowned Night Heron, *Nycticorax nycticorax* (Lorenz 1934, Tinbergen 1946).

The origin of the post-landing display is probably a composite of the recovery after landing and the preparation for either attack, defence, submission, or fleeing. Certainly birds which land at a crowded roost or colony and females landing beside an advertising male are frequently severely attacked. On the other hand a bird that has just landed may, after the post-landing display, charge rather violently to the side of its mate. *Morus bassanus*, *M. capensis*, and *M. serrator*, for example, frequently bite the head of the "in" bird on arrival at the nest (fig. 11), (Perry 1948, von Levetzow unpublished MS, Warham 1958). Cormorants on arrival at the nest often "paw" the back of the "in" bird with one of their feet. The head-biting of gannets and the back-pawing of cormorants may be derivatives of low intensity mounting.

The function of the post-landing displays is probably to facilitate individual and, in the Phalacrocoracidae,
species recognition by drawing the attention of actual and potential mates. It may also help to habituate birds from adjoining nests to each other and thus reduce the frequency of conflict between them. Dorward (1962) postulates that it may help to inhibit molestation, as Lorenz (1934) claims is the case for the post-landing posture of *N. nycticorax*.

No post-landing displays have been discovered in the families Pelecanidae, Fregatidae, and Phaethontidae. This may be due to a lack of observational data.

Gannets and Boobies

The post-landing posture is the same in the gannets, *Morus bassanus* (Stresemann 1953), and *M. serrator* (Warham 1958), and in the boobies *Sula sula*, *S. dactylatra*, and *S. leucogaster* (Dorward 1962). It consists of an arched neck, with the head close in front of the body, and the bill pointing downwards (fig. 12). It somewhat resembles the characteristic resting posture of pelicans (fig. 12). Warham (1958) calls it the post-landing version of the appeasement posture in *M. serrator*, and Dorward (1962) refers to it as the bill-tucking display in *S. dactylatra* and *S. leucogaster*. According to von Levetzow (unpublished MS), the neck and bill are erected vertically and a single call note is uttered by *M. capensis* after touching down. *Morus bassanus* and *Sula sula* are silent during the post-landing display.
Anhingas

In *A. anhinga*, the post-landing posture appears to be similar to its pre-take off posture.

Cormorants

The post-landing postures of the *Phalacrocoracidae* show in contrast to the *Sulidae* a high degree of inter-specific variation. *Ph. olivaceus* and *Ph. urile* during the post-landing postures hold their expanded heads and necks high with their bills pointing forwards (figs. 13 & 14). *Ph. carbo* displays its head discoidally by flattening it laterally and increasing it to its fullest extent in the sagittal plane. The bill is pointed forward and slightly downwards (fig. 13). This post-landing posture is called the "rooo" posture by Kortlandt (1938, 1949). In *Ph. carbo* and *Ph. olivaceus* the pre-take off postures as well as the post-landing postures are enhanced by the raised condition of the medial crest of the "out" bird, as opposed to the sleek condition of the head and neck of the "in" bird (figs. 7, 13 & 15).

*Ph. varius* bulges the gular pouch and raises the head and neck feathers after landing (Serventy and White 1943).
Ph. pelagicus raises but does not expand its head and neck, and points its bill forwards during the post-landing posture (fig. 14) (van Tets 1959). Ph. aristotelis raises its head and neck, and widely opens its bill skywards, thus exposing its yellow mouth lining (Selous 1901) (fig. 14). Ph. penicillatus, raises its head and neck, and by inflation flashes its bright blue gular pouch which is normally hidden. It also points its bill forward and slightly upwards during the post-landing posture (fig. 14) (van Tets 1959, Williams 1942).

Ph. auritus, during the post-landing posture holds its inflated head with the bill pointing forward, lower than its expanded and arched neck (fig. 13) (van Tets 1959). In this posture it closely resembles the twisted neck posture (Davis 1938, Davis and Friedmann 1936) of Ph. harrisi in which the "out" bird also holds its head with the bill pointing forward, lower than the arched neck. (fig. 13).

The call note some cormorants make during the post-landing display is absent in Ph. penicillatus and female Ph. aristotelis, and present in male Ph. aristotelis. It differs sexually in sound in Ph. carbo, but does not do so in Ph. auritus, Ph. urile, and Ph. pelagicus. According to Kortlandt (1938, 1949) the voice of the female Ph. carbo becomes masculine-like during the incubation period.
Fig. 11. Neck-grabbing during mounting in *Morus bassanus* (top), on return to nest in *M. bassanus* (middle), and in *M. capensis* (bottom). Bottom figure drawn from photograph in Gibson-Hill (1948), others drawn from photographs.
Fig. 12. Post-landing postures from top right to bottom left of *Morus bassanus*, *Sula sula*, *S. dactylatra*, and *S. leucogaster*.

Resting posture of *Pelecanus occidentalis*, bottom right.

*S. dactylatra* and *S. leucogaster* redrawn from Dorward (1962), others drawn from photographs.
Fig. 13. Post-landing postures of *Phalacrocorax carbo* (top right), *Ph. olivaceus* (middle left), and *Ph. auritus* (bottom left).

Twisted neck posture of *Ph. harrisi* (bottom right) drawn from photograph in Davis (1938).

Middle left redrawn from field sketch, others drawn from photographs.
Fig. 14. Post-landing postures of *Phalacrocorax urile* (top left), *Ph. penicillatus* (top right), *Ph. aristotelis* (bottom left), *Ph. pelagicus* (bottom right). Drawn from photographs.
Fig. 15. Median crest postures of *Phalacrocorax carbo*, withdrawn (top right), raised (bottom left). Drawn from photographs.
The "hop" is a characteristic display of gannets, boobies, anhingas, and cormorants. In essence it is an abbreviated symbolic flight which starts with a pre-flight display and ends with a post-landing posture. All gradations can be observed between flying from one part of the colony to another, "circle-flying" away and back to the nest site, hopping from one perch to the next, hopping only a few inches, and a pre-hop display followed by a post-hop display without the feet leaving the ground.

The hop as a display may help to draw the attention of the actual or potential mate on the nest site and of the nearby conspecifics. The hop display is often used during mounting and dismounting, when moving from the landing perch to the nest and vice versa, and when moving around the nest rim. Display hopping is done throughout the nesting season by the "out" bird until the nest is abandoned.

Pelicans, Pelecanus erythrorhynchos, P. occidentalis, P. onocrotalus, and P. crispus, have not been observed to hop. Phaethon lepturus does not stand up on its relatively short legs, and moves on land with an awkward waddle, or a series of hops (Plath 1913). It is unlikely that these hops of Ph. lepturus have any display function. At Half Moon Caye a male Fregata magnificens was seen making a clumsy flying hop between two perches six feet apart. No other hop-like acts were seen in this species. Probably the relatively short legs of the tropicbirds and frigatebirds prevent them
from using hopping for display purposes.

It is also possible that the lack of hop displays in the Pelecanidae, Fregatidae and Phaethontidae is due to the apparent lack of pre-take off and post-landing displays.

The pre-hop displays of the gannets, *Morus bassanus* and *M. serrator*, the Red-footed Booby, *S. sula*, the Anhinga, *A. anhinga*, and the cormorants, *Phalacrocorax carbo*, *Ph. auritus*, and *Ph. olivaceus* are the same as the pre-flight displays.

The four exclusively marine cormorants, *Ph. aristotelis*, *Ph. urile*, *Ph. pelagicus*, and *Ph. penicillatus* arch their necks and point their bills downwards during their pre-hop displays (figs. 8, 9, & 10). As in the pre-flight postures of these birds, the bills of *Ph. aristotelis*, *Ph. urile*, and *Ph. penicillatus* are closed, while the bill of *Ph. pelagicus* is wide open. During short hops of these species the head often remains down until the bird has landed again and the post-hop display is started.

The post-hop postures of the gannets, *Morus bassanus* and *M. serrator*, the Red-footed Booby, *S. sula*, the Anhinga, *A. anhinga*, and the cormorants, *Phalacrocorax carbo*, *Ph. auritus*, *Ph. olivaceus*, *Ph. aristotelis*, *Ph. urile*, *Ph. pelagicus*, and *Ph. penicillatus* are the same as the post-flight postures of these birds. Sometimes the post-hop display starts before the bird has touched down as in *Ph. aristotelis* and *Ph. penicillatus* (figs. 8 & 10).

The twisted neck posture (Davis 1938, Davis and Friedmann 1936) of the Flightless Cormorant, *Ph. harrisi* is
probably a post-hop posture closely related to that of Ph. auritus (fig. 13). Although Townsend (1929) mentions that Ph. harrisi is very proficient at hopping, he does not report any displays that either precede or follow the hopping.

The Cape Gannet, Morus capensis, steps around in a posture very similar in form to the look phase of the pre-take off and pre-hop posture of M. bassanus and M. serrator (figs. 3 & 4). After a few steps a squeaky rattling note is made (Gibson-Hill 1948). Tinbergen (1959b) calls this posture the "Schreckstellung" in M. capensis, and von Levetzow (unpublished MS) claims that this posture inhibits attack and is used by the bird on the nest to inhibit and prevent a neck bite from its returning mate (fig. 11). It is possible that the latter has confused this posture with the head-wagging display which sometimes starts with the bill pointing upwards (fig. 35).
Stepping.

While tree-nesting and cliff-nesting birds are limited in the amount of walking they can do near their nests, birds that nest in crowded colonies on flat ground often have to walk some distance to and from their nest after landing and before take off. Some of the Pelecaniformes like *Morus capensis*, *Sula variegata* and *Phalacrocorax bougainvillei* nest in some of the largest known sea-bird colonies on relatively flat ground (Gibson-Hill 1948, Murphy 1936), and often they have to run the gauntlet through dense aggregations of conspecifics to reach their own nest. While walking to and from their nests the gannets, boobies, and cormorants may use some of the displays which have been described in the earlier sections. Thus in *Morus capensis* one form of the sky-pointing is used for the pre-take off display and another for walking through the colony (Gibson-Hill 1948).

The walking draws attention to the brightly coloured feet of some species, and this effect is related apparently in *Sula nebouxii* and *S. variegata* to the evolution of a stepping display which is a part of the male advertising display. It consists of the male stepping around and in place near the nest site with the tail up and the down-cast head wagging from side to side. During the stepping display a gabbling sound is emitted. This stepping display usually precedes and follows the wing-waving or sky-pointing display (Beck 1904, Gifford 1913, Murphy 1936, Rothschild and Hartert 1902,
and Vogt 1942). According to Dorward (1962) the stepping display does not occur in *S. leucogaster* and *S. dactylatra*. He does record, however, a bill-up-face-away display of these species which resembles the head-flagging of some of the gulls (Tinbergen and Broekhuysen 1954, Tinbergen and Moynihan 1952) in form and function. *S. leucogaster* (fig. 1) and *S. dactylatra* perform the bill-up-face-away display when they walk towards their partner on the nest site. In this display the bill is raised and pointed away from the bird on the nest site. Sometimes the outside foot is also directed away from the nest site during the bill-up-face-away display (fig. 1).
Male-advertising.

Boobies, anhingas, and cormorants have male-advertising displays in common which are called sky-pointing (Dorward 1962) in the boobies, and wing-waving (Allen 1961) in anhingas and cormorants. In most species these displays consist of raising the wings by humeral rotation up and outwards. It is normally done by the male "in" bird on his nest site prior to the egg-laying by his mate. As is normal for an "in" bird the body axis is in a horizontal position during these displays when they are done at full intensity. This horizontal body posture is called either squatting or crouching by some authors (Harley 1946, Palmer 1962, Serventy and White 1943).

The extent to which the tail is raised during the sky-pointing and wing-waving displays appears to be related to the intensity of the display. The arc which includes the various tail elevations during these displays is given for some species in tables 1, 2 & 3. See also figure 16. These arcs tend to be species-specific and display-specific.

Some species, Sula sula, S.dactylatra, S.nebouxii, S.variegata, Phalacrocorax auritus, Ph.olivaceus, and Ph.varius, but not Ph.carbo, Ph.penicillatus, Ph.pelagicus, and Ph.urile, utter a characteristic call note each time the wings are raised. Sula leucogaster makes the call note but does not raise the wings. Phalacrocorax aristotelis neither calls nor raises the wings. Instead the males of these last two species advertise with the movements that
are associated with the wing-raising in the sky-pointing and wing-waving displays of the species most closely related to them.

No wing-waving displays have been observed in the Pelecanidae, Fregatidae, and Phaethontidae.
Fig. 16. Diagram showing the nine 30 degree sectors that were used for the frequency distributions of tail elevations in tables 1-3, 6-10, 12-15, 25 and 26.
Boobies.

The sky-pointing display of the boobies (fig. 16) appears to be a derivative of the pre-take off display of the gannets (figs. 3 & 4), for they have in common the same head and neck postures, a similar single call note, and except for *S. leucogaster*, a similar upward movement of the wing tips. However, instead of the tail remaining down as in the pre-take off of the gannets (figs. 3 & 4), the boobies raise their tails during the wing-waving displays (fig. 17 and table 1).

The boobies differ species-specifically in the distance their wing tips move apart when they are raised. In the Masked Booby, *S. dactylatra*, the wings move straight up while in the Red-footed Booby, *S. sula*, they move up and outwards (Dorward 1962). In these two species, as in the wing-waving of anhingas and cormorants, the primaries remain folded behind the secondaries when the wing tips are raised. In the Blue-footed Booby, *S. nebuluxii*, and in the Peruvian Booby, *S. variegata*, the primaries are opened out from behind the secondaries as the wing tips are raised and moved apart (fig. 17) (Beck 1904, Gifford 1913, Murphy 1936, Rothschild and Hartert 1902, and Vogt 1942).

According to Dorward (1962) the Brown Booby, *S. leucogaster*, occasionally performs the head and neck posture,
and the call note of the sky-pointing display while gliding near the colony. This may be a form of uncoordinated courtship. If it does, however, serve to lead a female to the cliff-side nests of this species, it may explain the loss of the wing component of the display.

The sky-pointing display has been called the four-point display by Verner (1961) in _S.sula_, and bowing by Gifford (1913) in _S.nebouxii_.
Anhingas.

The wing-waving display (Allen 1961) of the Anhinga, *A.anhinga*, is unique in that the wings are raised alternately as a repetitive movement two or more cycles per second (fig. 18). At low intensity according to Meyerrieks (Palmer 1962) the wing-waving starts with both wings moving up and down together as in the sky-pointing of boobies and the wing-waving of cormorants. During the wing-waving of the Anhinga the motion and position of the body, tail (table 1), and neck, as well as the rate of wing movement are not constant but vary a great deal (Allen 1961). The head and neck feathers including the median crest are raised during the wing-waving.

The wing-waving of *A.anhinga* has been called wing-flapping by Meanley (1954).
Cormorants.

The wing-waving of the cormorants, except for the Shag, *Ph. aristotelis*, consists of raising the wing tips simultaneously up and outwards with the primaries folded behind the secondaries (fig. 19). In some species, *Ph. carbo*, *Ph. urile*, *Ph. pelagicus*, and *Ph. penicillatus*, this movement is further emphasized by the exposure of a pair of white rump patches of nuptial plumes each time the wings are raised. White nuptial rump patches occur also in *Ph. capillatus*, *Ph. magellanicus*, *Ph. neglectus*, *Ph. fusescens*, *Ph. atriceps*, and *Ph. carunculatus* (Alexander 1955). In other species, *Ph. auritus* (Lewis 1929), *Ph. olivaceus*, and *Ph. varius* (Serventy and White 1943), a loud call note is emitted each time the wing tips are raised.

*Ph. melanoleucus* raises the wing tips only once per display (Harley 1946). *Ph. carbo*, *Ph. auritus*, *Ph. olivaceus*, *Ph. urile*, *Ph. pelagicus*, and *Ph. penicillatus* raise the wing tips repeatedly, many times per display, as is recorded for some of these species in table 4. The rate at which the wings are waved is less than twice per second in *Ph. carbo*, *Ph. auritus*, and *Ph. olivaceus*, and a rapid irregular flutter, faster than twice per second in *Ph. urile*, *Ph. pelagicus*, and *Ph. penicillatus*.

In *Ph. melanoleucus* there is a movement of the body
associated with the wing-waving display. The bird begins by standing erect. Next with the wings folded but held out from and slightly above the body, the bird squats and quickly returns to an erect position. This display is repeated a number of times. During the wing-waving the feathers are ruffled and the tail is elevated slightly (Harley 1946).

In Ph. carbo, Ph. auritus, Ph. olivaceus, Ph. varius (Serventy and White 1943), Ph. urile, Ph. pelagicus, and Ph. penicillatus the head is held above the back with the bill pointing upwards and forwards during the wing-waving, and is moved up and down at the same rate as the wing tips. The head moves down as the wing tips move up and vice versa. In the Shag, Ph. aristotelis, during the throw-back part (Cullen unpublished MS) of the male-advertising display, the head is similarly and with more emphasis moved rapidly up and down (table 4), while it is held above the back close to the base of the tail (fig. 18) (Selous 1901, van Beusekom 1953). The rate at which the head moves up and down resembles that of the head and wing tips in the wing-waving of the likewise exclusively marine cormorants Ph. urile, Ph. penicillatus, and Ph. pelagicus.

The wing-waving has been called "vleugel klappen" (wing-flapping) by Portielje (1927), Haverschmidt (1933), Kortlandt (1938, 1949) in Ph. carbo, singing by Lewis (1929) in Ph. auritus, and fluttering by Williams (1942) in Ph. penicillatus, and by Serventy and White (1943) in Ph. varius.
Table 1. Frequency Distributions of Tail Elevations during Sky-pointing, Wing-waving and Throw-back, for nine 30 degree sectors between downwards and forwards. See fig. 16.

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<tr>
<td>Avery Island, La.</td>
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</tr>
<tr>
<td><strong>Throw-back</strong></td>
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<td></td>
</tr>
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<td><em>Ph. aristotelis</em></td>
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<td>3</td>
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<tr>
<td>Farne Islands, England</td>
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Table 2. Frequency Distributions of Tail Elevations during Wing-waving in *Phalacrocorax carbo* for nine 30 degree sectors between downwards and forwards. See fig. 16.

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Table 3. Frequency Distributions of Tail Elevations during Wing-waving, for nine 30 degree sectors between downwards and forwards. See fig. 16.

<table>
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<td></td>
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</tbody>
</table>

| **Ph. olivaceus** |                        |
| Lacassine N.W.R., La. | 5  12                  |
|                    | 0                      |
|                    | 0                      |
|                    | 0                      |
|                    | 0                      |
|                    | 0                      |
|                    | 0                      |

| **Ph. pelagicus**  |                        |
| Mandarte Island, B.C. | 0  0                   |
|                    | 3                      |
|                    | 0                      |
|                    | 4                      |
|                    | 15                     |
|                    | 5                      |
Table 4. Frequency and Duration of Sky-pointing, Wing-waving, and Throw-back.

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<th>Cycles per display av. SD.</th>
<th>Seconds per display av. SD.</th>
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<tr>
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<td><em>Ph. auritus</em></td>
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<tr>
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<td>B.C.</td>
<td>wrist-watch</td>
<td></td>
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<td>4</td>
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<td>Throw-back</td>
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<td>2.8</td>
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Fig. 17. Sky-pointing of *Sula sula* (top left), *S. dactylatra* (top right), *S. leucogaster* (middle left), *S. nebouxii* (bottom). Bottom figure redrawn from Jaques in Murphy (1936), top right and middle left redrawn from Dorward (1962), top left drawn from photograph.
Fig. 18. *Anhinga anhinga*, wing-waving (top), snap-bowing (bottom left and right). Drawn from photographs.
Fig. 19. Wing-waving of *Phalacrocorax carbo* (top right), *Ph. auritus* (top left), *Ph. olivaceus* (middle right), *Ph. pelagicus* (middle left), and *Ph. penicillatus* (bottom right). Throw-back of *Ph. aristotelis* (bottom left). Drawn from photographs.
Fighting and its Derivatives.

Fighting.

Fighting in the order Pelecaniformes as in many other kinds of animals at the intra-specific level occurs normally between members of the same sex. Males fight for the possession of a nest, and females fight for a male and his nest site. In most colonies, Ph.auritus and Ph.pelagicus at Mandarte Island and Ph.aristotelis at the Farne Islands, Morus bassanus (Perry 1948), Ph.carbo (Kortlandt 1949), fights are a relatively rare event and tend to occur at those nest sites where the nest- and pair-bonds have not yet been firmly established. Fighting in these birds is of a defensive nature, and most fights start when either two males that have been using the same nest or two females that have been courting the same male meet on the nest for the first time. In Ph.carbo colonies with a limited number of nest sites, nestless males will occasionally try and sometimes initially succeed in evicting incubating females or undefended chicks from their nests. In the same circumstance a nestless female may try to oust a mated female from her nest and mate (Kortlandt 1949). An attempt at ousting a mated female by an unmated female was observed in Ph.aristotelis at the Farne Islands.

The fighting is done with the bill and not with the feet or with the angles of the wings. It consists of grabbing the opponent by the neck or the angle of the wing. Frequently the beaks are locked (fig. 20) (Kortlandt 1949,
A tugging and pushing bout follows in which each bird worries the other by using a sideways head-shaking movement. During the fighting the tail is raised and the wings are lowered and sometimes spread (fig. 20). The fight usually ends in the loser pulling free and fleeing, or in the antagonists tumbling locked together out of the nest. Sometimes several bouts over a period of one or more days are needed before the loser finally gives in, as was observed at the Farne Islands in Ph. aristotelis, and by Kortland (1949) in Ph. carbo.
Fig. 20. Fighting, *Phaethon aethereus* (top), and *Morus bassanus* (bottom). Top figure drawn from photograph in Stonehouse (1960). Bottom figure drawn from photograph.
Threat.

Threatening movements can be broken down into the following components: the posing of the head and neck ready for the strike, the movement of the head forwards, the opening of the bill, the closing of the bill, and the worrying of the opponent by the sideways-shaking of the head.

Threat signals usually consist of an elaboration of these components combined with a threat call. The threat indicates that there will be a fight if the intruder comes any closer, and thus damage that could be caused by actual combat may be avoided.

The pelicans, *Pelecanus occidentalis*, *P. erythrorhynchos*, *P. onocrotalus*, and *P. crispus* threaten by raising, opening, and subsequently waving their wide open bill at either passing pelicans and cormorants or at nest predators such as gulls and crows (fig. 21 & 22) (Bernatzik 1930, Meischner 1958, 1962, Schaller unpublished MS).

The gannets, *Morus bassanus*, *M. capensis*, *M. serrator*, and the boobies, *Sula sula*, *S. leucogaster*, *S. dactylatra*, *S. nebouxi*, and *S. variegata* threaten by either pointing their closed bills, or wagging their open bills while emitting a threat call, or lunging and snapping at birds and humans that come too close to their nests (fig. 22) (Cunningham 1866, Dorward 1962, Warham 1958, 1961, Murphy 1936, Verner 1961, Wetmore 1918).

The threat of the Anhinga, *A. anhinga*, at Avery Island, Louisiana, consists of either walking or hopping out
among the branches of the cypress tree which contains its nest, with the wings slightly spread and the bill open, towards the intruding Anhinga, or Common Egret, *Casmerodius albus*. This six to fifteen foot sortie away from the nest is quite unique among the pelecaniform birds which normally defend only the nest and an area not more than a neck length away from it. Snapping movements are made at intervals by the threatening anhinga at its opponent.

The cormorants vary a great deal in their threat displays (fig. 22). In *Phalacrocorax carbo*, *Ph. auritus*, *Ph. olivaceus*, and *Ph. varius* the neck is S-shaped, the throat is expanded, and the mouth is open. Usually the horns of the hyoid apparatus move apart. The head is moved irregularly from side to side and back and forth, while the bill faces towards the opponent. The threat call differs sexually in *Ph. carbo*, but not in *Ph. auritus*.

In *Ph. penicillatus* the head is repeatedly thrown forward in a rapid and irregular fashion (Williams 1942). A threat call that does not differ sexually is uttered. *Ph. aristotelis* with a similar motion flashes its yellow mouth lining at the intruders. The male but not the female of this species makes a loud threat call during the threat display.

There are two phases to the threat of *Ph. pelagicus*. First the head is repeatedly darted back and forth silently. Then the head is shaken in the withdrawn position with a gargling sound that is the same in both sexes. *Ph. urile*
has a threat similar in appearance and sound to *Ph. pelagicus*.

Neither intra-specific fighting nor threatening was noticed amongst the *Fregata magnificens* nesting at Half Moon Caye. During take off an adult male hit another male with his wing without any visible reaction. Only once a female on a nest was seen waving an open bill at a nearby Red-footed Booby, *Sula sula*. Warham (1961) describes *Fregata ariel* chicks as threatening by snapping at each other and by waving open bills while uttering repetitive call notes. Murphy *et al.* (1954) shows a photograph of a large *Fregata minor* chick directing an open bill at the hand of a nearby person. The lack of intra-specific aggressiveness in a genus that steals a large portion of its food and nest-material from other sea birds, confirms the observation by Lorenz (1952) in the chapter on morals and weapons, that the severity of intra-specific conflict is inversely related to the potential danger inherent in the "weapons" of a species.

The threat of the tropicbirds, *Phaethon lepturus*, *Ph. aethereus*, and *Ph. rubricauda* consists of pecking and screaming at tropicbirds and humans that "invade" their nest cavities (Gross 1912, Plath 1913, 1914, 1916, Stonehouse 1962b).
Fig. 21. *Pelecanus erythrorhynchos* threatening Herring Gull, *Larus argentatus*. Drawn from photograph.
Fig. 22. Threat postures of *Pelecanus crispus* (top), *P. erythrorhynchos* (top right), *Phalacrocorax penicillatus* (top middle left), *Ph. auritus* (bottom right), *Sula sula* (bottom middle left), *Morus bassanus* (bottom). Drawn from photographs.
Recognition.

The male advertising displays serve to attract females. To the males of a monogamous species only one female will be acceptable when the pair-bond is formed. Hence a signal to ward off unwanted females and another signal to recognize a desired female are needed by these males. A threat is usually sufficient to scare away the unwanted females. In the cormorants where an unacceptable female is often grabbed by the neck and heaved out of the nest soon after she lands, the females usually hop cautiously towards an alternately advertising and threatening male. If a female is very persistent the threats may by habituation become less and less violent until eventually their very mildness indicates that she may be tolerated at the nest. Thus some of the recognition displays may have arisen from the various components of the threat displays (compare figs. 22 - 27).

Other recognition displays seem to have been derived from nest-building and food-begging movements, and these will be described in later sections. No threat derivatives have been reported as recognition displays in the frigatebirds and tropicbirds.
Pelicans

The pelicans, *Pelecanus occidentalis*, *P. erythrorhynchos*, *P. onocrotalus* and *P. crispus* have a bisexual display of both the "in" and the "out" bird, the bill-raising. This display consists of raising the closed bill with the gular pouch expanded (figs. 23 & 24). It is directed both at the mate and the chicks in the nest as well as at pelicans on nearby nests. Some authors consider this a threat display (Bernatzik 1930, Meischner 1958, 1962), while others regard it as a courtship display (Schaller unpublished MS). It is probably a very mild threat which also serves as a recognition display between nest mates and neighbours. When nesting on the ground, *P. occidentalis* and *P. erythrorhynchos*, normally have their nests less than pecking distance apart and in small groups (Murphy 1936, Schaller unpublished MS). Grinnel (1908) recorded the average distance between nest centers for *P. erythrorhynchos* to be 1380 mm. with a minimum of 828 mm. He found also that 828 mm. is the maximum reaching distance away from the nest for scraping in nest material.

The closeness of the nests may help to reduce nest predation by birds smaller and more agile than the pelicans, for example gulls, night herons, crows, and grackles. On the other hand, the pelicans have to tolerate the close proximity of not only their nest mates but also their neighbours.
Fig. 23. Bill raising with gular pouch expansion in *Pelecanus onocrotalus* (top), *P. erythrorhynchos* (bottom). Drawn from photographs.
Fig. 24. Bill-raising in *Pelecanus crispus* without pouch expansion (top right), with pouch expansion (middle and bottom). Middle figure drawn from photograph in Meischner (1958), and bottom figure drawn from photograph in Meischner (1962). Top figure drawn from photograph.
Boobies.

At Half Moon Caye, British Honduras, the Red-footed Booby, *Sula sula*, was seen to have a head-throwing display which is a bisexual recognition display of the "in" bird. The head-throwing consists of moving the head forward and back silently with the bill closed (fig. 25). Similar displays have not been reported in the gannets or in any of the other species of boobies.

The frequency and duration of the head-throwing display is given in table 5, and the frequency distribution of the tail elevations during this display in table 6.
Cormorants.

Cormorants have a gape display in which the head is moved in the median plane and the bill is opened at the climax of the display (figs. 25, 26 & 27). Like the head-throwing of Sula sula the gape is a bisexual recognition display of the "in" bird. In it, various components of fighting and threatening are greatly modified and formalized. The frequency and duration of the gape display is recorded for some species in table 5 and the frequency distribution of tail elevations in tables 6, 7, 8 & 9.

The call note made during the gape is sexually different in Ph.carbo, Ph.urile and Ph.pelagicus, sexually similar in Ph.auritus and Ph.penicillatus, and present in male but not female Ph.aristotelis. The movements of the gape display are sexually diethic in Ph.carbo, and sexually monocethic in Ph.auritus, Ph.olivaceus, Ph.aristotelis, Ph.urile, Ph.pelagicus, and Ph.penicillatus.

In Ph.carbo and Ph.aristotelis the head is swung back and in Ph.urile, Ph.pelagicus, and Ph.penicillatus the head is swung forward before the mouth opens for the gape. Ph.auritus and Ph.olivaceus stretch the neck upwards, and sway their necks slowly with the bill wide open.

Ph.carbo, Ph.auritus, Ph.olivaceus, Ph.aristotelis, and Ph.penicillatus open their bills once per display, while
Ph. pelagicus and Ph. urile open their bills several times per display, once at the end of each upward movement of the head. During the gape display the head moves up and down about twice per second in the last two species. The females of Ph. urile and Ph. pelagicus alternate between two call notes like the ticking of the pendulum of a "grandfather clock", while the males make the same "purring" call note each time the bill is opened.

The backward movement of the head continues during the gape and after the bill closes in the male but not the female Ph. carbo until the base of the tail is reached (fig. 26). Here the bill is shaken sideways with a gargling sound that resembles the threat call of Ph. pelagicus and Ph. urile. During the opening of the bill the males of Ph. carbo, make the same "purring" call note as the males of Ph. urile and Ph. pelagicus make during their gape displays.

In Ph. aristotelis the body is shaken and often tends to become vertical during the gape display (fig. 27). As a result of becoming upright the gape display resembles the post-landing and post-hop display of this species. The body is not shaken, however, in the post-landing and post-hop display and in the male the post-landing and post-hop call differs from the call note made during the gape display.

The brilliantly blue gular patch is expanded throughout the gape display of Ph. penicillatus. The swollen head is "cocked" backwards before the head is moved rapidly forward. The bill is not opened as widely as in the gape
display of the other cormorant species when it reaches the forward position (fig. 25).

The gape display has been called the click-gape by Cullen (unpublished MS) in *Ph. aristotelis*, the stroke by Williams (1942) in *Ph. penicillatus*, and "gorgelen" (gargling) by Kortlandt (1938, 1949) in *Ph. carbo*. 
Table 5. Frequency and Duration of Gaping, Darting, and Head-throwing.

<table>
<thead>
<tr>
<th>Display</th>
<th>Species</th>
<th>Sex</th>
<th>Loc.</th>
<th>Film speed f.p.s.</th>
<th>Number of displays</th>
<th>Cycles per display av.</th>
<th>Seconds per display av.</th>
<th>Cycles per second av.</th>
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<tr>
<td></td>
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<td>1</td>
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<td>0.4</td>
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<tr>
<td></td>
<td></td>
<td>♂</td>
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<td>16</td>
<td>6</td>
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<td>1.8</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>♂</td>
<td>Holland</td>
<td>16</td>
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<td>3.0</td>
<td>0.6</td>
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<tr>
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<td></td>
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<td>P.E.I.</td>
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<td>1</td>
<td>2.8</td>
<td>0.3</td>
</tr>
<tr>
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<td></td>
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<td>16</td>
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<td>2.3</td>
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<td>2</td>
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<td>6.6</td>
<td>2.9</td>
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<td>2.0</td>
<td>0.6</td>
</tr>
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<td></td>
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<td>6</td>
<td>1</td>
<td>1.6</td>
<td>0.5</td>
</tr>
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<td>2.2</td>
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Table 6. Frequency Distributions of Tail Elevations during Gaping, Darting, and Head-throwing, for nine 30 degree sectors between downwards and forwards. See fig. 16.

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Table 7. Frequency Distributions of Tail Elevations during Gaping in *Phalacrocorax carbo* males, for nine 30 degree sectors between downwards and forwards. See fig. 16.

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<thead>
<tr>
<th>Location</th>
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<th>Downwards (30°)</th>
<th>Downwards (60°)</th>
<th>Downwards (90°)</th>
<th>Forwards (0°)</th>
<th>Forwards (30°)</th>
<th>Forwards (60°)</th>
<th>Forwards (90°)</th>
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<td>0</td>
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</tr>
<tr>
<td>Farne Islands, England</td>
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### Table 8. Frequency Distributions of Tail Elevations during Gaping, for nine 30 degree sectors between downwards and forwards. See fig. 16.

<table>
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<th>Species</th>
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</tr>
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</tr>
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Table 9. Frequency Distributions of Tail Elevations during Gaping in *Phalacrocorax aristotelis* for nine 30 degree sectors between downwards and forwards. See fig. 16.

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Fig. 25. Starting (left) and extended (right) positions of, from top to bottom, head-throwing in *Sula sula*, darting in *Phalacrocorax aristotelis*, gaping in *Ph. penicillatus*, and gaping in *Ph. pelagicus*. Drawn from photographs.
Fig. 26. Gaping of *Phalacrocorax carbo*, starting (left, top) and extended (right top) of female, successive positions of male, lateral view (left middle to right bottom) and frontal view (right middle). Drawn from photographs.
Fig. 27. Gaping of *Phalacrocorax auritus* (top left and right), *Ph. olivaceus* (middle), and *Ph. aristotelis* (bottom left and right). Middle figure redrawn from field sketch, others from photographs.
Pointing

The pointing display of some cormorant species is a bisexual display of the "in" bird. In *Ph. carbo*, *Ph. auritus*, *Ph. olivaceus*, *Ph. varius*, and *Ph. penicillatus* it consists of stretching the neck, head, and closed bill forward and upward (fig. 28). No sound is made. In this position the head and neck are waved slowly and the tail is raised (fig. 28 and table 10).

The origin of the pointing display may either be an extreme reduction of the gape and threat displays or possibly a vestige of the sky-pointing of the Sulidae. It is not a pre-copulation display as is suggested by Williams (1942). It does, however, occur like the other recognition displays before, after, and sometimes during mounting in the "in" bird.

The pointing has been called "nek-zwaaien" (neck-swaying) by Kortlandt (1938, 1949) in *Ph. carbo*, the pre-coititional posture by Williams (1942) in *Ph. penicillatus*, and the low crouching attitude by Serventy and White (1943) in *Ph. varius*. 

Table 10. Frequency Distributions of Tail Elevations during Pointing in *Phalacrocorax carbo* Males, for nine 30 degree sectors between downwards and forwards. See fig. 16.

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</table>
Fig. 28. Pointing of _Phalacrocorax carbo_ (top left), _Ph. auritus_ (middle right), _Ph. olivaceus_ (middle left), and _Ph. penicillatus_ (bottom). Top figure from photograph, others from field sketches.
Male-advertising.

Darting.

As the bisexual pre-take off display of gannets seems to have given rise to the masculine sky-pointing of boobies, so also does the bisexual threat display of the Shag, *Phalacrocorax aristotelis*, appear to have given rise to the darting display (Cullen unpublished MS) of the males of this species as "in" birds on their nest sites.

This display consists of moving the head rapidly and horizontally back and forth (fig. 25 and table 5). In the forward position the bill opens and the yellow mouth lining is flashed. Apparently no sound is made. The tail is raised (table 6). The darting differs from the threat of this species in that the darting movement is confined to the median plane and is more formal and regular.

The darting precedes the throw-back in the male-advertising display in *Ph. aristotelis* but does not form a part of the male-advertising displays of *Ph. carbo*, *Ph. auritus*, *Ph. olivaceus*, *Ph. urile*, *Ph. pelagicus*, and *Ph. penicillatus*. It closely resembles the first component of the threat of *Ph. pelagicus*, which is a bisexual display of both the "in" bird and the "out" bird, and does not include the flashing of the mouth lining.
Pointing.

Besides the alternate wing-waving, the male-advertising of the Anhinga, *A. anhinga*, as an "in" bird also includes the pointing (Allen 1961). In it, as in the bisexual pointing of some cormorants, the male Anhinga stretches the neck, head, and closed bill forward and upward and waves them slowly. The throat is flattened laterally (Allen 1961). Unlike the wing-waving and the bow, the head and feathers are not raised and the bird has a sleek appearance. The tail is raised (fig. 29).

The origin of the pointing is doubtful but is probably the same in both the anhingas and in the cormorants. It may have been derived from either a threat display or from the head, neck and bill posture in the sky-pointing of the Sulidae.
Fig. 29. *Anhinga anhinga* males pointing (top) and kink-throating (bottom). Top figure drawn from photograph and bottom figure redrawn from field sketch.
Nest-building and its Derivatives.

Nest construction.

The type and size of nest, if any, that is built by a pair of pelecaniform birds depends on the species, the nest site and the available materials. Nest types include scrapes, mounds, and stick nests. Stick nests are constructed mainly of sticks, twigs, and pieces of wood, and may be either on the ground or in trees and bushes. Stick nests are normally made by species that frequently or almost always nest arboreally, *Pelecanus rufescens*, *P. crispus*, *P. philippensis*, *P. occidentalis*, *Sula sula*, *S. abbotti*, *Anhinga anhinga*, *A. rufe*, *Phalacrocorax carbo*, *Ph. fuscicollis*, *Ph. sulcirostris*, *Ph. varius*, *Ph. auritus*, *Ph. olivaceus*, *Ph. africanus*, *Ph. pygmaeus*, *Ph. niger*, and *Ph. melanoleucus*.

At ground-nesting and cliff-nesting colonies the nests of the arboreal species can be recognized by the high incidence of sticks in the nest material. At Mandarte Island where *Phalacrocorax auritus* and *Ph. pelagicus* nest on the same cliffs and collect most of their nest material from the same ground and the same drift lines on the sea only *Ph. auritus* includes sticks in its nest-material. Only a small fraction of these twigs were obtained by breaking them off the branches of trees, a source of supply not available to *Ph. pelagicus* which neither nests nor perches in trees.

Some species such as the Brown Pelican and the Double-crested Cormorant may make practically no nest at
all when nesting on the ground (Forbes 1914, McLeod and Bondar 1953, Murphy 1936, Sprunt 1925), while these same species will build very elaborate nests in trees (Bailey 1947, Beck 1904, Eibl-Eibesfeldt 1960). In situations where there is sufficient nest material, however, their ground nests may become as large or even larger than their tree nests (Anthony 1889, Behle 1958, Grinnel 1908, Sprunt 1925).

Many species - all three tropicbirds, three out of seven pelicans, all three gannets, four out of six boobies, no anhingas, eighteen out of twenty eight cormorants, and no frigatebirds - appear to lack the inclination or ability to nest on branches of trees. Some of these ground-nesters, Morus bassanus, M. serrator, Sula leucogaster, Pelecanus erythrorhynchos, P. onocrotalus, P. conspicillatus, Phalacrocorax capillatus, Ph. capensis, Ph. harrisi, Ph. punctatus, and Ph. featherstoni include sticks in their nest structure. Others such as Morus capensis, Sula dactylatra, S. nebouxii, S. variegata, Phalacrocorax aristotelis, Ph. urile, Ph. pelagicus, and Ph. penicillatus do not build stick nests, but do perform the same movements with stray feathers, twigs, and dry algae as related species use to insert sticks into the nest rim (Dorward 1962, Gibson-Hill 1948, Murphy 1936, van Tets 1959). Contrary to Palmer (1962) it is Sula abbotti, and not S. dactylatra, that nests or nested in trees at the Seychelles and Christmas Islands, Indian Ocean (Alexander 1955, Vesey-Fitzgerald 1941, Vesey-Fitzgerald and Betts 1940).
The droppings of some cliff-nesting species, such as *Phalacrocorax pelagicus*, help to cement the outside of the nest consisting of a mixture of hay, grass, and algae to the cliff face (Jones 1909, van Tets 1959). This species, at Mandarte Island, like the Kittiwake, *Rissa tridactyla*, at the Farne Islands assembles in large numbers to pull up fresh grass for their nests after the ground has been softened by rain.

The tropicbirds lay their eggs mainly in cavities and show no nest-building activities at all (Gross 1912, Lowe 1909, MacGillivray 1918, Plath 1916, Stonehouse 1960, 1962b).

It appears from the above that parallel reductions in nest-building have occurred in the exclusively ground-nesting forms of the Pelecanidae, Sulidae, and Phalacrocoracidae from a tree-nesting common ancestor. Some of the cormorants have evolved cliff-nesting methods, while the tropicbirds have become cavity-nesters, in which no trace of nest-building habits can be found.

During courtship and pair-formation nest material is brought to the nest site by the males of *Morus bassanus*, *M. capensis*, *Sula sula*, *S. leucogaster*, *S. dactylatra*, *A. anhinga*, *Phalacrocorax carbo*, *Ph. auritus*, *Ph. pelagicus*, *Ph. urile*, *Ph. aristotelis*, *Ph. penicillatus*, *Fregata magnificens*, and *F. minor* (Courtenay-Latimer 1954, Dorward 1962, Gallagher 1960, Gifford 1913, Murphy et al 1954, Reithmuller 1931, Worcester 1911a), and not by the females
as suggested for the Fregatidae, and *F. magnificens* in particular, by Murphy (1938, 1939) and quoted by Van Tyne and Berger (1959) (see table 11).

Later when the pair-bond is well established, the females will also fetch some nest material as part of the nest relief ceremonies in *Morus bassanus*, *M. serrator*, *A. anhinga*, *Phalacrocorax carbo*, *Ph. auritus*, *Ph. harrisi*, and *Ph. pelagicus* (Eibl-Eibesfeldt 1960, Kortlandt 1949, and Warham 1958).

In those species that build stick nests, both sexes work sticks and other items into the nest structure. Even while alone on the nest they will frequently try to secure loose nest material more tightly. The male starts to gather nest material before he is mated, but the nest-building does not become effective until a female starts to guard the nest site during his absence against nest material thieves. The addition of new material to the nest does not cease until after the chicks have fledged. The older chicks of some species, *Morus bassanus*, *Phalacrocorax auritus*, and *Ph. pelagicus* help in the securing of fresh material that is brought in by the parents, into the nest structure (Perry 1948, van Tets 1959).

Sticks, pieces of wood, plant stalks, feathers, and other rigid materials are inserted with a sideways shaking of the head into the nest rim at an approximately 45° angle to the horizontal.

The "in" birds also reach out with the bill to draw in loose material from around the nest. On the ground this action produces the mound nests with the circular scraped
perimeter outside the nest edge (Dorward 1962, Gifford 1913, Grinnel 1908, Murphy 1936, 1955).
Table 11. Sexual Differences in Nest Material-fetching.

<table>
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<tr>
<th>Species</th>
<th>No. of times nest material brought to nest by male</th>
<th>No. of nests</th>
<th>Dates</th>
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<td>1</td>
<td>29Apr. - 30Apr.'61</td>
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<tr>
<td>Ph.carbo</td>
<td>62</td>
<td>0</td>
<td>9Febr. - 22Mar.'62</td>
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<tr>
<td>Ph.auritus</td>
<td>87</td>
<td>7</td>
<td>27Apr. - 14Sept.'59</td>
</tr>
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<td>Ph.aristotelis</td>
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<td>31Mar. - 28Apr.'62</td>
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<tr>
<td>F.magnificens</td>
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<td>25Dec.'60 - 1Jan.'61</td>
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</table>
Defensive nest-indicating.

Like many other kinds of animals, the Pelecaniformes defend their nests more tenaciously than other perching sites. It is not surprising, therefore, that nest-indicating movements often alternate with threat movements in these and other birds. These nest-indicating movements consist of drawing in nearby objects, worrying nest material and nearby vegetation, prodding the bill into the nest structure, and merely pointing the bill downwards.

The survival value of the defensive nest-indicating movements may be the emphasizing of the nest and thus the informing of conspecifics and possibly other intruders that more is being claimed than just perching space. The origin and at times the motivation of these movements may well be also a redirection of defensive fighting movements as suggested by Tinbergen (1953).
Recognition and Bowing.

Just as some recognition displays appear to be ritualised versions of threat and fighting movements, other recognition displays seem to have been derived from the nest-building and nest-worrying movements.

Least formal and widely spread throughout the Pelecaniformes except for the Phaethontidae, is the presentation and passing back and forth of nest material. This is not only done between members of a courting pair but also among sibling chicks, between chicks and parents, and between pen mates in zoos. This mutual "handling" and "playing" with nest material probably tends to promote and strengthen the social bonds between them.

Most formal and with a limited distribution in the Pelecaniformes are the various bowing displays. These displays have in common an arched neck with the bill pointing down and in some species backwards.

Several types of bowing displays probably evolved independently by parallel evolution from nest-building movements in the Pelecaniformes. More than one form of bowing occurs in Pelecanus erythrorhynchos. Some of the bowing displays closely follow and a few have acquired attributes from one of the other displays.
Pelicans

The American White Pelican, *Pelecanus erythrorhynchos*, at Stum Lake was observed to have a sexually diethic display of both the "in" and the "out" bird, the reach-bowing, which consists of moving the head forward with the closed bill pointing downwards and the gular pouch expanded. During this movement the crown of the male's head is held higher and of the female's head lower than the top of the back (fig. 30). Sometimes a piece of nest material is picked up when the head reaches the extended position. The movement seems to be a derivative of the reaching out for nest material. The display serves probably as an aid to sex recognition by emphasizing the size differences between males and females, and as a recognition display between pair members. Grinnel (1908) mentions radiating spoke-like grooves around the nests in the sand. He interprets these grooves as being bill marks.

Schaller (in press) reports a similar display, the wave-bowing in this species. In it the head, with the gular pouch expanded and the closed bill pointing at the feet, is waved from side to side. No forward movement of the head, or any sexual differences were noted in this display. Schaller's description suggests that the wave-bowing is a derivative of the worrying of a stick into the nest structure.

At North Island, Mississippi delta, Louisiana, an
adult Brown Pelican, *P. occidentalis*, after landing beside its nest containing two large chicks, moved its head forward and upward without tipping the bill upwards as in the bill-raising display. The bill remained pointing down and somewhat forward and the gular pouch was expanded. Nelson (1911) photographed this reach-bowing display during the nest relief at a nest containing two small chicks (fig. 30). This display may be related to the reach-bowing of *P. erythrorhynchos*. 
Fig. 30. Reach-bowing of *Pelecanus erythrorhynchos* male (top) and female (middle), and of *P. occidentalis* (bottom). Bottom figure drawn from photograph in Nelson (1911), others redrawn from field sketches.
Gannets.

The gannets, *Morus bassanus*, *M. capensis*, and *M. serrator*, have a wing-bowing display, in which the closed bill moves down beside the flank and is pointed down and backwards (fig. 31) (Broekhuysen and Rudebeck 1951, Courtenay-Latimer 1954, Gibson-Hill 1948, Perry 1948, 1951, and Warham 1958). This display is bisexual and occurs in both the "in" bird and the "out" bird. No sound is made. The frequency distributions of tail elevations during the wing-bowing are recorded in table 12 and the duration of the display is given in table 16.
Boobies.

The boobies *Sula leucogaster* and *S. dactylatra* have a quiver-bowing display in which the tail is up, the body is horizontal, the neck is arched, and the tip of the bill almost touches the ground, is slightly open, and is quivered (fig. 31) (Dorward 1962, and photographs in Worcester 1911a, 1911b). The quiver-bowing is a bisexual display of both the "in" and the "out" bird. Sometimes during mutual quiver-bowing the necks of a pair are crossed as in the mutual reach-bowing of *Pelecanus erythrorhynchos*. Dorward (1962) found a gradual gradation between the quiver-bowing and the depositing of nest material.

*S. leucogaster* has also a side-bowing display in which the "in" bird alternately bows to the left side and to the right side, and occasionally to the front (Warham 1961). This is a bisexual display which apparently serves as a mild threat and as a recognition display. Like the wing-bowing of the gannets, the side-bowing is also closely linked with the head-wagging display (Warham 1961). The side-bowing of *S. leucogaster* may be either homologous to the head-wagging of *S. sula* or intermediate between it and the combined head-wagging and wing-bowing of gannets (see the section on head-wagging later in the text).

The Red-footed Booby, *S. sula* has a bisexual front-bowing display which is done by the "in" bird (Verner 1961).
In this display the closed bill is pointed silently down at the nest (fig. 31). In the male the front-bowing often follows the sky-pointing (table 29) (Verner 1961). The wings may then sometimes remain in the raised position (fig. 31). The frequency distribution of tail elevations during front-bowing is recorded in table 13 and the duration of the display is given in table 16.
The snap-bow display of *A. anhinga* is a bisexual display of the "in" bird (Allen 1961). The snap-bow consists of a nearby twig being grabbed with the bill and shaken vigorously with a sideways wagging of the head. During this the wings with the primaries folded behind the secondaries are raised by humeral rotation up and outwards, the tail is raised up and sometimes forward, (table 13), and the head and neck feathers including the median crests in the male are erected (fig. 18). Meanley (1954) reports that a call note is made at the climax of this display.

Often the bird will snap at a non-existing twig while assuming the snap-bow posture. This apparently has led Meyerrieks (Palmer 1962) to call this display the forward-snap. The snap-bow display of *A. anhinga* does in fact show many similarities to the well known snap display of the Ardeidae (Baerends and Baerends-van Roon 1960, Baerends and van der Cingel 1962, Cottrille and Cottrille 1958, Meyerrieks 1960, Palmer 1962, Verwey 1930).

The snap-bow display of the Anhinga seems to be derived from a fusion of a front-bow display with the wing-waving display. A similar fusion sometimes occurs in the male Red-footed Booby, *Sula sula* (Verner 1961) (fig. 31). Unlike the repetitive alternative wing-waving
of the Anhinga, the snap-bowing of the Anhinga seems to have retained the single simultaneous wing-waving movement of the male boobies.
Cormorants.

The Little Pied Cormorant, *Phalacrocorax melanoleucus*, has a gape-bowing display. In this display the bird begins by standing very erect. It then thrusts its neck out to full length, immediately swings its head and neck, and to a certain extent its body, downward and opens its bill wide. These movements bring the head to its perch or onto the nest. Thereafter the bird retracts its neck and returns to an erect posture. During this gape-bowing display an intermittent cooing sound is often made. The display only takes a matter of seconds and seems to be repeated with occasional pauses of a few seconds (Harley 1946).

This gape-bowing display of *P. melanoleucus*, may be related to the gaping displays of the other cormorants; it also shows in its raising and lowering of the body a strong resemblance to the snap display of the Ardeidae (Baerends and Baerends-van Roon 1960, Cottrille and Cottrille 1958, Meyerrieks 1960, Palmer 1962, Verwey 1930).

The Shag, *Ph. aristotelis*, has a bisexual front-bowing display which is performed by the "in" bird. In it the closed bill is pointed silently down underneath the breast at the nest site (fig. 31). In the male Shag the front-bowing follows the throw-back part of the male
advertising display. In the female Shag it often occurs before, during, and after mounting. The frequency distribution of tail elevations during the front-bowing is recorded in table 13, and the duration of the display in table 16.

Ph. carbo, Ph. auritus, and Ph. pelagicus do not have formal bowing displays. These species as well as Ph. aristotelis alternate the social displays of the "in" bird with bouts of nest-worrying (tables 17 - 23). The frequency distributions of tail elevations during nest-worrying in these species are recorded in tables 14 and 15, and the durations of the displays are recorded in table 16.
Fig. 31. Front-bowing in *Sula sula*, wings down (top left) and wings up (top right), quiver-bowing in *S. leucogaster* (middle top right), front-bowing *Phalacrocorax aristotelis* (bottom left and right), and wing-bowing in *Morus bassanus* (middle left and right). *Sula leucogaster* drawn from photograph in Worcester (1911b), others drawn from photographs.
Table 12. Frequency Distributions of Tail Elevations during Wing-bowing in *Morus bassanus* at Bonaventure Island, P.Q. for nine 30 degree sectors between downwards and forwards. See fig. 16.

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<td>Two on nest site.</td>
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Table 13. Frequency Distributions of Tail Elevations during Bowing, for nine 30 degree sectors between downwards and forwards. See fig. 16.

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<th>Front-bowing,</th>
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<td>Ph. aristotelis males</td>
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Table 14. Frequency Distributions of Tail Elevations during Nest-worrying. See fig. 16. There are nine 30 degree sectors between downwards and forwards.

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<tr>
<th>Species</th>
<th>Frequency Distributions</th>
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<tr>
<td>Ph. pelagicus Males, Mandarte Island, BC.</td>
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</tr>
<tr>
<td>Ph. aristotelis Females, Farne Islands, England.</td>
<td>0 0 0 0 3 0 2 0 0</td>
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Table 15. Frequency Distributions of Tail Elevations during Nest-worrying in *Phalacrocorax carbo* for nine 30 degree sectors between downwards and forwards. See fig. 16.

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</tr>
<tr>
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<td>0</td>
<td></td>
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<td></td>
<td></td>
</tr>
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<td></td>
<td>3</td>
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<td></td>
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<tr>
<td></td>
<td></td>
<td>3</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
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<td></td>
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<td></td>
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</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
<td></td>
<td></td>
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</tbody>
</table>
Table 16.  Duration of Bowing and Nest-worrying.

<table>
<thead>
<tr>
<th>Display</th>
<th>Species</th>
<th>Sex</th>
<th>Loc.</th>
<th>Film speed f.p.s.</th>
<th>Number of displays</th>
<th>Seconds per displays av. SD.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing-bowing</td>
<td><em>M. bassanus</em></td>
<td>(one on nest site)</td>
<td>P.Q.</td>
<td>24</td>
<td>29</td>
<td>1.1 1.3</td>
</tr>
<tr>
<td></td>
<td>&quot; &quot;</td>
<td>(two on nest site)</td>
<td>P.Q.</td>
<td>24</td>
<td>3</td>
<td>1.5 0.8</td>
</tr>
<tr>
<td>Front-bowing</td>
<td><em>S. sula</em></td>
<td>male</td>
<td>B.H.</td>
<td>16</td>
<td>27</td>
<td>1.8 1.2</td>
</tr>
<tr>
<td>Nest-worrying</td>
<td><em>Ph. aristotelis</em></td>
<td>male</td>
<td>England</td>
<td>16</td>
<td>3</td>
<td>3.1 0.2</td>
</tr>
<tr>
<td></td>
<td>&quot; &quot;</td>
<td>female</td>
<td>England</td>
<td>16</td>
<td>4</td>
<td>2.4 1.1</td>
</tr>
<tr>
<td></td>
<td><em>Ph. carbo</em></td>
<td>male</td>
<td>P.E.I.</td>
<td>24</td>
<td>1</td>
<td>2.1</td>
</tr>
<tr>
<td></td>
<td>&quot; &quot;</td>
<td>male</td>
<td>England</td>
<td>16</td>
<td>9</td>
<td>2.7 1.2</td>
</tr>
<tr>
<td></td>
<td>&quot; &quot;</td>
<td>male</td>
<td>Holland</td>
<td>16</td>
<td>2</td>
<td>3.8 0.7</td>
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<tr>
<td></td>
<td>&quot; &quot;</td>
<td>female</td>
<td>P.E.I.</td>
<td>24</td>
<td>1</td>
<td>1.8</td>
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<tr>
<td></td>
<td>&quot; &quot;</td>
<td>female</td>
<td>Holland</td>
<td>16</td>
<td>12</td>
<td>2.3 1.2</td>
</tr>
<tr>
<td></td>
<td><em>Ph. auritus</em></td>
<td>male</td>
<td>B.C.</td>
<td>24</td>
<td>5</td>
<td>2.9 1.1</td>
</tr>
<tr>
<td></td>
<td><em>Ph. pelagicus</em></td>
<td>male</td>
<td>B.C.</td>
<td>24</td>
<td>13</td>
<td>2.1 1.2</td>
</tr>
<tr>
<td></td>
<td>&quot; &quot;</td>
<td>male</td>
<td>B.C.</td>
<td>16</td>
<td>24</td>
<td>2.7 2.5</td>
</tr>
</tbody>
</table>
Table 17. Sequential Chart of *Ph. carbo* Males alone on Nest Site, Farne Islands, England, showing number of times the various behaviour patterns followed each other on an 8 mm. film.

<table>
<thead>
<tr>
<th>Follows</th>
<th>Wing-waving</th>
<th>Gaping</th>
<th>Pointing</th>
<th>Nest-worrying</th>
<th>Threat</th>
<th>Resting</th>
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<tbody>
<tr>
<td>Wing-waving</td>
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<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Gaping</td>
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<td>0</td>
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<td>1</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Pointing</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>4</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Nest-worrying</td>
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<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
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<td>1</td>
<td>1</td>
<td>0</td>
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Table 18. Sequential Chart of *Ph. carbo* Males alone on Nest Site, Naardermeer, Holland, showing the number of times the various behaviour patterns followed each other on an 8 mm. film.

<table>
<thead>
<tr>
<th>FOLLOWS</th>
<th>Wing-waving</th>
<th>Gaping</th>
<th>Pointing</th>
<th>Nest-worrying</th>
<th>Resting</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing-waving</td>
<td>0</td>
<td>6</td>
<td>1</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Gaping</td>
<td>5</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pointing</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Nest-worrying</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Resting</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
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</table>
Table 19. Sequential Chart of *Ph. carbo* Females on Nest Site, male present, Naardermeer, Holland, showing the number of times the various behaviour patterns follow each other on a 8 mm. film.

<table>
<thead>
<tr>
<th></th>
<th>Gaping</th>
<th>Nest-worrying</th>
<th>Resting</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gaping</td>
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<td>9</td>
<td>0</td>
</tr>
<tr>
<td>Nest-worrying</td>
<td>6</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>Resting</td>
<td>1</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 20. Sequential Chart of *Ph. auritus* Males alone on Nest Site, Mandarte Island, B.C., Canada, showing the number of times the various behaviour patterns follow each other on a 16 mm. film.

<table>
<thead>
<tr>
<th></th>
<th>Wing- waving</th>
<th>Gaping</th>
<th>Nest- worrying</th>
<th>Threat</th>
<th>Resting</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing- waving</td>
<td>0</td>
<td>1</td>
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<td>1</td>
</tr>
<tr>
<td>Gaping</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Nest- worrying</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>2</td>
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<td>Threat</td>
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<td>1</td>
<td>0</td>
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</table>
Table 21. Sequential Chart of Ph. aristotelis Females on Nest Site, male present, Farne Islands, England, showing the number of times the various behaviour patterns follow each other on an 8 mm. film.

FOLLOWS

<table>
<thead>
<tr>
<th></th>
<th>Gaping</th>
<th>Front-bowing</th>
<th>Nest-worrying</th>
<th>Threat</th>
<th>Resting</th>
</tr>
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<tr>
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<td>4</td>
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<td>5</td>
</tr>
<tr>
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<td>0</td>
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<td>Nest-worrying</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Threat</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Resting</td>
<td>7</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>0</td>
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</table>
Table 22. Sequential Chart of *Ph. pelagicus* Males on Nest Site, female present, Mandarte Island, B.C. Canada, showing number of times various behaviour patterns follow each other on an 8 mm. film.

<table>
<thead>
<tr>
<th></th>
<th>Gaping</th>
<th>Nest-worrying</th>
<th>Resting</th>
</tr>
</thead>
<tbody>
<tr>
<td>PRE</td>
<td>Gaping</td>
<td>0</td>
<td>11</td>
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<tr>
<td>CDE</td>
<td>Nest-worrying</td>
<td>11</td>
<td>0</td>
</tr>
<tr>
<td>S</td>
<td>Resting</td>
<td>0</td>
<td>2</td>
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Table 23. Sequential Chart of *Ph. pelagicus* Males alone on Nest Site, Mandarte Island, B.C., Canada, showing the number of times the various behaviour patterns follow each other on an 8 and a 16 mm. film.

<table>
<thead>
<tr>
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<th>Threat</th>
<th>Resting</th>
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<tbody>
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<tr>
<td>Gaping</td>
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<td>0</td>
<td>4</td>
<td>1</td>
<td>4</td>
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<tr>
<td>Nest-worrying</td>
<td>1</td>
<td>4</td>
<td>0</td>
<td>14</td>
<td>5</td>
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<tr>
<td>Threat</td>
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<tr>
<td>Resting</td>
<td>6</td>
<td>2</td>
<td>5</td>
<td>4</td>
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</table>
Begging and its Derivatives.

Food-begging.

The chicks of the Pelecaniformes, unlike the nestlings of the Passeriformes, beg for food with closed bills (fig. 32 & 33). This is usually accompanied by a repetitive call note. During the first few days after hatching the head is raised and waved from side to side. After the eyes have opened the begging is oriented towards the head of the parent. Once the chick is large enough it prods the gular pouch of the parent, and the sideways waving of the head begins to grade into head-wagging. For further emphasis during the begging the chicks often spread their wings and move them back and forth in a plane perpendicular to the long axis of the body. During begging the body axis may be either horizontal or upright but it is usually the latter just before the chick is fed. The fledglings of *Fregata magnificens* at Half Moon Caye, British Honduras, spread their tails as well as their wings during food-begging.

The chicks of all the Pelecaniformes feed on regurgitated food by inserting their heads into the mouths of their parents (figs. 32 & 33) (Allen 1961, Bailey and Wright 1931, Chapman 1908, Fisher 1904b, Lorenz 1935, Oberholser 1938, Perry 1948, Stonehouse 1962b, Stresemann 1927 - 1934, van Dobben 1952, and Warham 1958). This method of food-transfer from parent to chick is order-specific and unlike the methods used in related taxa. Thus the chicks
of albatrosses, fulmars, and herons insert usually no more than their bills into the bill of their parents (Fisher 1952, Lowe 1954, Rice and Kenyon 1962, and Richdale 1952).

The begging of cormorant and anhinga chicks is further characterized by a forward movement of the hyoid apparatus which gives the gular pouch an angular appearance (figs. 32 & 33) (Kortlandt 1940, photograph in Oberholser 1938, van Tets 1959).
Fig. 32. Food-begging of *Sula leucogaster* fledgling (top left), *S. dactylatra* fledgling (top right), and *Anhinga anhinga* nestling (bottom left), feeding of nestling by parent (from top to bottom) of *Morus bassanus*, *Pelecanus erythrorhynchos*, and *A. anhinga*. Top left figure redrawn from Dorward (1962), top right figure redrawn from Stonehouse (1960), pelican drawn from photographs by Bailey and Niedrach in Behle (1958), bottom figure drawn from photograph by Bailey and Dickinson in Oberholser (1938). *M. bassanus* drawn from photograph.
Fig. 33. *Phalacrocorax auritus*, water-begging (top left and right), food-begging (middle left), feeding by parent of nestling (middle right) and fledging (bottom left). Drawn from photographs.
Water-begging.

During periods of warm dry weather *Phalacrocorax carbo* and *Ph. auritus* bring water to their nestlings. The chicks of these two species beg for water by waving their wide-open bills upwards (fig. 33). The parent pours the water from its almost but not quite closed bill into the wide open mouths of the chicks. (Kortlandt 1949, Schuster 1935, van Dobben 1952, and van Tets 1959).

At Mandarte Island, British Columbia, where *Ph. auritus* and *Ph. pelagicus* nest together in the same colony only *Ph. auritus* was seen bringing water to its nestlings. In *Ph. auritus* the water is usually brought to the begging chicks by the parent going "off duty" after nest relief. At Mandarte Island the "old guard", instead of fetching nest material, will glide down to the sea and gulp up several mouthfuls of seawater. Within one minute the bird is back at the nest pouring water down the throats of its offspring. In *Ph. auritus* the water-begging display resembles the gape display. Apparently as a result of this the water carrier sometimes is also seen pouring some water down the throat of its mate. Single adults at the nest are often seen responding to the water-begging by putting their closed bills in the mouths of the chicks, without any transfer of either fluid or solid matter being noted. This may be an inadequate response resulting from the strong inhibition to desert the nest.
Recognition.

One of the first social signals that a young pelecaniform bird uses is food-begging. In pelicans, boobies, cormorants, and frigatebirds, but not gannets, food-begging is often, even after fledging, the response of a chick to the sight of one of its parents at and away from the nest (Ferry 1910, Kortlandt 1949, Perry 1948, Stonehouse 1960, van Tets 1959, Warham 1958, 1961). It is not surprising, therefore, that some of the recognition displays of the adults resemble the food-begging of the chicks.

In many kinds of birds the begging for and the presentation of food forms a major part of the courtship and pair-forming ritual (Tinbergen 1952a). In the Pelecaniformes the male neither gives nor presents food to the female. Only Gross (1912) reports having seen one adult Phaëthon lepturus feed another adult during incubation on the nest. The Pelecaniformes present only nest material to their mates. This is done by the male during the courting and pair-forming. Later the female may also present nest material as part of the nest relief ceremonies (table 11). During the "handling" of the nest material both sexes use displays and associated call notes which resemble components of food-begging. These displays are also used before landing, and in some species as the main recognition and male advertising displays.

In their bisexual use of food-begging derivatives the Pelecaniformes resemble the Larinae, in which both sexes
signal with modified food-begging displays prior to both the courtship-feeding and the mounting of the female by the male (Tinbergen 1952b, 1959a).
Pelicans.

At Stum Lake, B.C. *Pelecanus erythrorhynchos* sometimes expanded the gular pouch before landing and while circle-flying above the nesting colony (fig. 34). Finley (1907) reports that this species makes a rumbling noise before landing. At Stum Lake the birds were too far away from the point of observation for a study of their voices.

This aerial display may be related to the pre-landing version of the head-wagging of gannets and boobies, the kink-throating of anhingas and cormorants, the rattling of frigatebirds and the aerial display of tropicbirds as described in the following sections.
Fig. 34. Aerial pouch expansion in *Pelecanus erythrorhynchos*. Drawn from photographs.
Gannets.

One of the main displays of the gannets, *Morus bassanus*, *M. capensis*, and *M. serrator* is the head-wagging display (figs. 35 & 36) (Broekhuysen & Rudebeck 1951, Courtenay-Latimer 1954, Gibson-Hill 1948, Gurney 1913, Perry 1948, 1951, von Levetzow unpublished MS, and Warham 1958). The head-wagging of gannets consists of a characteristic sideways wagging of the head with the bill closed and the neck remaining in the median plane. During the head wagging the bill also moves slowly up and down from pointing almost vertically upwards to pointing almost vertically downwards in mid swing. At high intensity the whole body rocks back and forth and the angles of the wings move outwards with the wing tips often remaining folded over the base of the tail. The frequency and duration of head-wagging is given in table 24 and the frequency distribution of tail elevations in table 25. During the head-wagging a loud repetitive call note is made which does not differ sexually, but instead shows a great deal of individual specificity. This call note may be the main aid to individual recognition in this genus, for the plumage of adult gannets is remarkably uniform as compared to the other pelecaniform genera.

The head-wagging is done before and after landing, and at the nest site by both members of a pair, alone and
together, throughout the nesting season (Perry 1948, 1951, Warham 1958). At Bonaventure Island Northern Gannets were seen head-wagging actively with downy chicks at their feet. The head-wagging also accompanies the handling of nest material.

The head-wagging and the wing-bowing displays often closely follow and alternate with each other (tables 27 & 28), and appear to be two phases of the same display. The close affinities of the combined head-shaking and wing-bowing displays to nest-building movements was noticed in *M. bassanus* by Lorenz (1937) and Perry (1948, 1951), and in *M. capensis* by von Levetzow (unpublished MS). Warham (1958) calls the head-wagging without the wing-bowing the greeting ceremony, and the two displays together the curtsey, in *M. serrator*. At Bonaventure Island, P.Q., a period of alternating head-wagging and wing-bowing of a bird alone on a nest site was often terminated by a prolonged period of neck-preening (fig. 35, and table 27). Seven neck-preening bouts had an average duration of 5.8 seconds with a standard deviation of 2.5 seconds as measured with 16 mm. black and white film at 24 frames per second. The tail is not raised during the neck-preening, (table 26).

Often a pair of gannets will perform the head-wagging and wing-bowing displays in time and as mirror images facing each other on the nest (fig. 36). It then seems to serve as a mutual recognition display. The head-wagging of a single bird on the nest may serve to help in
guiding its mate back to the nest and may also serve as a male advertising display. The head-wagging of the landing bird may help to announce its impending arrival back at the nest. Nelson (1963) claims to have found a sexual difference in the head-wagging of marked *M. bassanus* at Bass Rock in Scotland.
Fig. 35. Head-wagging in *Sula dactylatra* (top left), *S. sula* (middle left and right), *Morus bassanus* (bottom left), and *M. serrator* (bottom right).

Neck-preening in *M. bassanus* (top right). Top left figure redrawn from Dorward (1962), bottom right figure drawn from photograph by Warham (1958), others drawn from photographs.
Fig. 36. Mutual head-wagging in *Morus capensis* (top), and *M. bassanus* (bottom). Top figure drawn from photograph in Gibson-Hill (1948), bottom figure drawn from photographs.
Table 24. Frequency and Duration of Head-wagging.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number on nest site</th>
<th>Loc.</th>
<th>Film speed f.p.s.</th>
<th>Number of displays</th>
<th>Cycles per display av. SD.</th>
<th>Seconds per display av. SD.</th>
<th>Cycles per second av. SD.</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. bassanus</em></td>
<td>one</td>
<td>P.Q.</td>
<td>24</td>
<td>39</td>
<td>3.1 1.4</td>
<td>1.0 0.3</td>
<td>3.2 1.2</td>
</tr>
<tr>
<td><em>M. bassanus</em></td>
<td>two</td>
<td>P.Q.</td>
<td>24</td>
<td>21</td>
<td>7.5 7.4</td>
<td>2.9 2.7</td>
<td>2.7 0.7</td>
</tr>
<tr>
<td><em>S. sula</em></td>
<td>one</td>
<td>B.H.</td>
<td>16</td>
<td>9</td>
<td>7 6</td>
<td>18 11</td>
<td>0.4 0.1</td>
</tr>
</tbody>
</table>
Table 25. Frequency Distributions of Tail Elevations during Head-wagging, for nine 30 degree sectors between downwards and forwards. See fig. 16.

<table>
<thead>
<tr>
<th>Species</th>
<th>One on Nest Site</th>
<th>Two on Nest Site</th>
</tr>
</thead>
<tbody>
<tr>
<td>Morus bassanus</td>
<td>0 0</td>
<td>0 0</td>
</tr>
<tr>
<td>Bonaventure Island, P.Q.</td>
<td>0 0</td>
<td>0 0</td>
</tr>
<tr>
<td></td>
<td>0 0</td>
<td>0 0</td>
</tr>
<tr>
<td></td>
<td>0 0</td>
<td>0 0</td>
</tr>
<tr>
<td></td>
<td>0 0</td>
<td>0 0</td>
</tr>
<tr>
<td></td>
<td>0 0</td>
<td>0 0</td>
</tr>
<tr>
<td></td>
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<td></td>
<td>0 0</td>
<td>0 0</td>
</tr>
<tr>
<td></td>
<td>0 0</td>
<td>0 0</td>
</tr>
<tr>
<td>Sula sula Male</td>
<td>8 0</td>
<td>0 0</td>
</tr>
<tr>
<td>Half Moon Caye, B.H.</td>
<td>5 0</td>
<td>0 0</td>
</tr>
<tr>
<td></td>
<td>2 0</td>
<td>0 0</td>
</tr>
<tr>
<td></td>
<td>0 0</td>
<td>0 0</td>
</tr>
<tr>
<td></td>
<td>0 0</td>
<td>0 0</td>
</tr>
</tbody>
</table>
Table 26. Frequency Distributions of Tail Elevations during Neck-preening in *Morus bassanus* at Bonaventure Island, P.Q. for nine 30 degree sectors between downwards and forwards. See fig. 16.

<table>
<thead>
<tr>
<th>Sectors</th>
<th>0</th>
<th>0</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
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<td>0</td>
</tr>
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<td>0</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0</td>
</tr>
</tbody>
</table>

One on nest site.
Table 27. Sequential Chart of M. bassanus, one on Nest Site, Bonaventure Island, P.Q., Canada, showing the number of times the behaviour patterns follow each other on a 16 mm. film.

<table>
<thead>
<tr>
<th></th>
<th>Head-wagging</th>
<th>Wing-bowing</th>
<th>Neck-preening</th>
<th>Threat</th>
<th>Resting</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head-wagging</td>
<td>0</td>
<td>28</td>
<td>7</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Wing-bowing</td>
<td>26</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Neck-preening</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Threat</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Resting</td>
<td>6</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 28. Sequential Chart of *M. bassanus*, two on Nest Site, Bonaventure Island, F.Q., Canada, showing the number of times the various behaviour patterns follow each other on a 16 mm. film.

<table>
<thead>
<tr>
<th>PRECEDES</th>
<th>Head-wagging</th>
<th>Wing-bowing</th>
<th>Resting</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head-wagging</td>
<td>0</td>
<td>4</td>
<td>15</td>
</tr>
<tr>
<td>Wing-bowing</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Resting</td>
<td>12</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Boobies.

The Red-footed Booby, *S. sula*, at Half Moon Caye, has a head-wagging display similar to that of the gannets in movement and sound. During its head-wagging not only the bill but also the head and neck swing from side to side, and at full intensity the bill dips down beside the feet alternately on one side and then the other (fig. 35). Unlike the gannets, however, the tail is raised during the head-wagging (table 25), and swings probably for balance from side to side in time with the head-wagging.

In the Red-footed Booby the head-wagging is a bisexual display of the "out" bird and is used by the "in" bird only when it is alone on the nest. The head-wagging then often alternates with a hop instead of with a wing-bow as in gannets (table 27, 28, & 29). As was noticed by Gifford (1913) and Verner (1961), *S. sula* uses the head-wagging also before and after landing, and frequently when holding some nest material in its beak.

Head-wagging displays have also been reported for some of the other *Sula* species. According to Warham (1961) *Sula leucogaster* has a mild greeting ceremony in which both members of a pair waggle their beaks and then dip their beaks to one flank as if picking up nest material. A similar movement is used as a threat towards humans in
which with a see-saw rhythm they poke at the nest material in front of them and at the earth behind them, or they alternate between dipping to the right and to the left. Usually the tail is cocked up and fanned at right angles to the body. Clearly this set of displays is related to the head-wagging and bowing of gannets and Red-footed Boobies but needs further study.

Dorward (1962) describes for *S. leucogaster* and *S. dactylatra* (fig. 35), and Vogt (1942) for *S. variegata* a head-wagging display in which only the bill moves from side to side as in the gannets. Vogt (1942) also describes a figure 8 movement of the bill tip as it moves up and down as well as from side to side during the head-wagging of *S. variegata*. Warham (1961) calls the head-wagging "head-waggling" in *S. leucogaster*. 
Table 29. Sequential Chart of *S. sula* males alone on Nest Site, Half Moon Caye, British Honduras, showing the number of times the various behaviour patterns follow each other on an 8 mm. film.

<table>
<thead>
<tr>
<th>PRECEDENCE</th>
<th>Sky-pointing</th>
<th>Head-throwing</th>
<th>Head-wagging</th>
<th>Front-bowing</th>
<th>Hop</th>
<th>Threat</th>
<th>Resting</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sky-pointing</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>10</td>
<td>0</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Head-throwing</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>16</td>
</tr>
<tr>
<td>Head-wagging</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Front-bowing</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>Hop</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Threat</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Resting</td>
<td>3</td>
<td>16</td>
<td>0</td>
<td>11</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Anhingas.

The kink-throat display of *A.anhinga* is a bisexual display of both the "in" and the "out" bird. When there is no nest material being held in the bill, the mouth is wide open and wagged from side to side (fig. 29). The female then displays her pink mouth lining and the male his black mouth lining. Both sexes utter a repetitive call note during this display (Owre 1962). The hyoid apparatus is pushed forwards and downwards as in the begging of the chicks while the neck is held in an S-shaped position and the open mouth is directed forward. In the male the median crest is partially raised (fig. 29).

The kink-throat display is used before landing, during the "handling" of nest material, and as a mutual recognition display at the nest. It is very prominent as a display during nest relief.
Cormorants.

The kink-throat display of the cormorants, *Phalacrococorax carbo*, *Ph. auritus*, *Ph. olivaceus*, *Ph. aristotelis*, *Ph. urile*, *Ph. pelagicus*, *Ph. penicillatus* is chiefly a bisexual pre-landing display (fig. 37). At the nest site it is used by both the "in" and the "out" bird during the "handling" of nest material (fig. 37). In *Ph. carbo* and *Ph. aristotelis* it occurs also as an intention movement prior to the look phase of the pre-take off and the pre-hop displays. Photographs 33 and 34 in Eibl-Eibesfeldt (1960) show the kink-throat display in both members of a pair of *Ph. harrisi* during the presentation of nest material by the "out" bird to the "in" bird.

In the cormorants as in the anhingas the kink-throat display is characterized by the forward depression of the hyoid apparatus. Unlike the anhingas, however, the cormorants normally have the bill closed during this display. Exceptions are *Ph. carbo* and *Ph. aristotelis* which kink-throat with the bill wide open during the pre-landing display, provided they are not carrying any nest material. On land and water these two species perform the kink-throat display with the bill closed.

The repetitive call note of the kink-throat display is species-specific. It differs sexually in *Ph. carbo*,
is audible 30 feet away in the male but not the female Ph. aristotelis, and does not differ sexually in Ph. auritus, Ph. urile, Ph. pelagicus, and Ph. penicillatus. The kink-throat display has been called the "kro kro" expression by Kortlandt (1938, 1949) in Ph. carbo.
Fig. 37. Kink-throating before landing (top and middle) and during nest-worrying (bottom) in *Phalacrocorax auritus*. Drawn from photographs.
Frigatebirds.

The rattling display of the frigatebirds, *Fregata magnificens*, *F.minor*, *F.aquila*, and *F.ariel*, is a sexually diethic display which is performed both in the air and on the nest by both sexes (Dill 1916, Fisher 1904a, 1906, Gallagher 1960, Kirby 1925, Lister 1891, Murphy 1936, 1939, and Stonehouse 1960). During the rattling the "gular sac" of the male is usually inflated (fig. 38). The repetitive sound of the rattling display is in part produced by the rattling together of the mandibles as is reported by Lister (1891) for *F.ariel*, Gallagher (1960) for *F.minor*, and Verner (Palmer 1962) for *F.magnificens*. According to Warham (1961) *F.ariel* also "clappers" with its mandibles when alarmed.

At Half Moon Caye the sound of the rattling display in *F.magnificens* was noticed to be of two forms in the male and of another in the female. These differences may be due to the male's "gular sac" acting as a resonator for one of his calls. The low intensity form of the male call is similar in sound to the clicking of a Red-footed Booby's mandibles as it preens its breast feathers.

During the rattling display of a *F.magnificens* male which is alone on the nest site the wings and the deeply forked tail are spread out laterally as in the food-begging of the chicks of this species. The wings are then fluttered
back and forth in a plane at right angles to the long axis of the body. The rate of the wing movement was measured with an 8 mm. colour film at 16 frames per second to be 4.6 cycles per second for a display of 38 cycles, and 3.1 cycles per second for a display of 22 cycles.

When the male and the female rattle together on the nest they usually sit side by side facing in opposite directions and with the wings closed. During this the male rattles with the bill pointed upwards and the female with the bill pointed downwards.

Gallagher (1960) reports the _F._minor males also spread their tails and wings during the rattling display.

The rattling display of the frigatebirds apparently serves as a mutual recognition display, as a male advertising and sex-recognition display, and as an announcement of imminent arrival at the nest.

Like the head-wagging of the boobies and gannets, and the kink-throating of the anhingas and cormorants, the rattling of the frigatebirds is also done during the "handling" of nest material. The rattling of the mandibles in the Fregatidae closely resembles the clappering of the Diomedeidae (Rice and Kenyon 1962, Richdale 1950). According to Jameson (1958) the clappering display is followed by the transfer of oil during the courtship of the Wandering Albatross, _Diomedea exulans_. Rice and Kenyon (1962) state that the newly hatched chicks of _D._immutabilis and _D._nigripes are
fed exclusively with stomach oil. This resemblance between the form and derivation of the rattling of the Fregatidae and the clappering of the Diomedeidae may support the close anatomical relationship Lanham (1947) found between the Fregatidae and the Procellariiformes.
Fig. 38. Rattling of *Fregata magnificens* Males in the air (top), before landing (middle), and on the nest (bottom). Drawn from photographs.
Tropicbirds.

The Tropicbirds, *Phaethon lepturus*, *Ph.aethereus*, and *Ph.rubricauda* have an aerial display (fig. 39 & 40) with a species-specific repetitive call, during which the birds alternately fly, glide and hover (Bailey 1956, Brattstrom and Howell 1956, Chaffer 1936, Gallagher 1960, Hadden 1941, Iredale 1910, Munro 1944, Murphy et al 1954, Plath 1916, Stonehouse 1960, 1962b, Warham 1961, and Worth 1935). During the hovering phase the tail is depressed and in *Ph.rubricauda* (Udvardy unpublished MS) the black feet are spread and brought close to the black tertial under coverts (fig. 39). When a pair display together, the upper bird during the hovering touches the lower bird with its elongated middle rectrices in *Ph.lepturus* (Worth 1935).

Hull (1909) noted a resemblance between the aerial call notes of *Ph.rubricauda* and the "Solan Goose" (*Morus*). Often the aerial display ends with a landing at the nest where the call note of the aerial display is continued. Gross (1912) noted that *Ph.lepturus* also makes a clicking sound before it lands at its nest to feed its chick.

It appears that because of the hidden nature of the nest site the courtship and pair-formation of the tropicbirds has become airborne. The only other aerial displays known from the Pelecaniformes are the aerial
display of *Pelecanus erythrorhynchos*, the post-take off displays of gannets and cormorants, the sky-pointing of *Sula leucogaster*, the pre-landing versions of the head-wagging of gannets and boobies, the kink-throating of anhingas and cormorants, and the rattling of frigatebirds. In the Pelecaniformes the head and bill tend to be up during the take off and down during the landing. During the aerial display of the tropicbirds the head and bill point downwards (fig. 39 & 40). The lowering of the tail during the aerial display's hovering phase resembles the way in which gannets and boobies lower their tails while they hover above their nests before landing. It therefore appears that the aerial display of the tropicbirds is closely related to the pre-landing displays of the pelecaniform birds. It may serve consequently as a nest site indicating display as well as a mutual recognition display and a male-advertising display. Analogous displays have been found in such cavity-nesting birds as ducks (Heinroth 1911) and the Pied Flycatcher, *Muscicapa hypoleuca* (von Haartman 1956, 1957).
Fig. 39. Aerial display of Phaethon rubricauda, gliding with feet away from black tertiary under coverts (top and bottom), hovering with feet close to black under coverts (middle left and right). Figures drawn from film of Laysan Island by M.D.F. Udvardy.
Fig. 40. Aerial display of *Phaethon lepturus* (top), and *Ph.aethereus* (bottom).

Top figure redrawn from Plath (1916), bottom figure drawn from photograph in Stonehouse (1962b).
Discussion.

Components of communication patterns.

In general the explicitness and effectiveness of a signal depends on its distinctiveness. Consequently when a display of a species begins to convey biologically meaningful information the forces of natural selection should tend to reduce its variability and increase its differences from other postures and movements of the species and from similar displays of related species. Thus selection may well be the extrinsic factor underlying Darwin's (1872) principle of antithesis which he postulated to be caused by intrinsic factors.

In the Pelecaniformes a number of distinct postures and movements of the various parts of their anatomy as well as a number of call notes are used in several combinations to form the communication patterns that have been described above.

Body.

The body of the Pelecaniformes is an oblong, and by pivoting it in the vertical plane the anhingas and cormorants, and to a lesser extent the boobies, achieve the contrast between the "out" bird with an upright posture and the "in" bird with a horizontal body posture. The horizontal body posture also occurs during incubating, fighting, take off, and in the lower bird during mounting. Neither motivation nor derivation can therefore be drawn from the body posture.
alone. It does, however, add information to a signal.

*Phalacrocorax melanoleucus* emphasizes its wing-waving and gape-bowing displays by switching from a vertical to a horizontal body posture, in a manner analogous to the way some of the Ardeidae lower and raise their bodies to emphasize their stretch and snap displays (Baerends G.P. and van der Cingel 1962, Meyerrieks 1960, Verwey 1930).

*Phalacrocorax aristotelis* shakes its body during its click-gape display in which, unlike the gape displays of the other cormorants, the body tends to become vertical. This shaking helps to differentiate the click-gape from the very similar post-landing display of this species in which the shaking does not occur.

Head and neck.

The neck is used to move the head in several characteristic patterns, one of the most elaborate being the gape display of *Phalacrocorax carbo* males. Almost all the head and neck movements during the social signals of the Pelecaniformes are in the median plane. The exceptions, such as the wing-bowing of gannets and the head moving down beside the body during the gape and wing-waving displays, appear to be due to the body being in the way, and in some cases a response and partial orientation towards the lateral location of the other bird. In the head-wagging of *Sula sula* the head and neck move from side to side. In the threat
displays and the alarm postures the head and neck movements tend to be much more irregular than the other displays, except for the begging displays of the chicks.

During the display postures the neck may be either arched as in the bowing displays of pelicans, gannets, boobies, anhingas and cormorants, in the post-hop postures of _Phalacrocorax auritus_ and _Ph. harrisi_, and the pre-hop postures of _Ph. aristotelis_, _Ph. penicillatus_, _Ph. urile_, and _Ph. pelagicus_, or straight as in the sky-pointing of gannets and boobies, and the pointing display of anhingas and cormorants. The sky-pointing differs from the pointing in the first being a vertical straight neck posture and the second being a variable straight neck posture. The neck is also straight in the gaping of _Ph. auritus_ and _Ph. olivaceus_.

Bill.

The movements of the head receive their emphasis from the bill which may be swung in the vertical plane as in the bill-raising of pelicans or sideways as in the head-wagging of gannets and boobies. During a display the position of the bill may be either up as in the male or down as in the female _Fregata magnificens_ during the rattling display on the nest.

A sideways pointing away of the bill as occurs in some of the gulls (Tinbergen and Broekhuysen 1954, Tinbergen and Moynihan 1952), finds its counterpart in the bill-up-
face-away display of *Sula dactylatra* and *S. leucogaster*. The sky-pointing and the bill-tucking displays of the Sulidae may well derive the bill up and the bill down components from a facing-the-bill-away movement as is suggested by Dorward (1962) and Warham (1958).

The forward position of the bill as in many of the post-landing and post-hop display of the cormorants, may in contrast to the appeasing role of the up, down, or sideways positions, have an intimidating role as suggested for the post-landing posture of *Phalacrocorax carbo* by Kortlandt (1949).

The wide open condition of the bill occurs in the threat and recognition displays of many species; it also occurs in the pre-take off display of *Phalacrocorax pelagicus*, the pre-landing display of *A. anhinga* and *Ph. carbo*, the post-landing display of *Ph. aristotelis*, the water-begging of *Ph. carbo* and *Ph. auritus*, and the bowing of *Ph. melanoleucus*. These displays are enhanced by the brilliant colouration of the mouth lining in many species. These colourations may also play a directing role in the feeding of the chicks which occurs inside the mouth and throat of the parent in the Pelecaniformes. In some displays such as the darting of *Ph. aristotelis* and the gaping of *Ph. urile* and *Ph. pelagicus* the mouth lining is flashed repetitively.

Gular region.

The "gular sac" plays both a visual and a resonating
role in the rattling display of the males of the Fregatidae. In *Pelecanus erythrorhynchos* the expanded gular pouch acts as a "flag" to emphasize the bill-raising, reach-bowing, wave-bowing, and aerial displays. The exposure of the gular pouch by bulging it outwards is a major feature of the post-landing and the gape displays of *Phalacrocorax penicillatus*. In many but not all cormorant species the expansion of the throat and gular pouch is a component of the pre-take off and the post-landing postures. The expanded condition contrasts with the not expanded condition. The post-landing posture of *Ph. carbo* has a unique lateral flattening and medial expansion of the head and throat region.

The forward movement of the hyoid apparatus into the contracted gular pouch produces the kink-throat configuration which characterizes the food-begging and kink-throat displays of cormorants and anhingas. Many cormorant species spread the horns of the hyoid apparatus during threat and thus increase the size of the head. A rapid vibration of the horns, the gular flutter, is part of an evaporative cooling mechanism of many avian taxa, and is very prominent in the Pelecaniformes except for the Phaethontidae (Bartholomew and Dawson 1954, Howell and Bartholomew 1962, Portielje 1927).
Wings.

On land the wings may be rotated forward as in the sun-bathing of Fregata aquila (Stonehouse 1960), or backwards as in the sky-pointing of the Sulidae, the wing-waving of the Anhingidae and the Phalacrocoracidae, and the snap-bowing of Anhinga anhinga. With or without forward or backward rotation the wings may be spread out fully, as in the sun-bathing of F. aquila (forward rotation), the sky-pointing of Sula nebouxii and S. variegata (backward rotation), and as in the rattling of male Fregata magnificens and the begging of pelecaniform chicks (no rotation). The wings are spread fully and raised about 30° in the pre-take off display of Morus capensis.

A partial spreading of the wings with the primaries folded behind the secondaries, together with backward rotation occurs in most of the sky-pointing and wing-waving displays of the Sulidae, Anhingidae and Phalacrocoracidae. In the Anhinga the alternate movement of its wing-waving contrasts with the simultaneous movement of the wings in the snap-bowing display of this species, and in the sky-pointing of the boobies and the wing-waving of the cormorants. Sula leucogaster and Phalacrocorax aristotelis have apparently evolved distinctive male-advertising displays which do not include the raising of the wing tips, but which are clearly homologous to displays in which related species do move their wings. The rates at which the cormorants raise and lower their wings during the wing-waving is about twice as rapid in the
marine species *Ph. urile*, *Ph. pelagicus* and *Ph. penicillatus* than in the continental species *Ph. carbo*, *Ph. auritus* and *Ph. olivaceus*.

The wings are lowered and sometimes spread during fighting and threat. Little or no rotation occurs then.

The wings may be spread out partially with no rotation during low intensity begging of the chicks, during the "spread-eagle" wing-drying, and during the pre-take off and the post-landing postures of the Anhinga. In an extended condition the wings may be waved back and forth in a transverse plane during wing-drying, in chicks during high intensity food-begging, and in *Fregata magnificens* males during the rattling display on the nest. The Pelecaniformes have as comfort movements the same stretching to one side and stretching upward of the wings as other birds (Heinroth 1917).

During the warm weather the Pelecaniformes spread the bends of their wings out laterally with the wing tips remaining folded over the base of the tail. This posture is frequently also a feature of the head-wagging and bowing displays of the gannets. It is not yet clear whether in the gannets the moving out of the wings is a functional part of the signal pattern or a response to temperature.

Tail.

The tail is raised during many of the displays of the "in" bird in boobies, anhingas, and cormorants. It
is also raised during some of the walking and stepping displays of some of the boobies. The height to which the tail is raised depends on the display, and the species (tables 1-3, 6-10, 12-15, 25, 26). The tail is also raised during fighting and threat, and by the female during copulation. The tail is lowered prior to landing, while hovering near the nest, and in the tropicbirds by the upper bird during the aerial display. The tail is also lowered by the male during copulation.

The tail moves up and down during the balancing on an unsteady perch, but an up and down movement apparently does not occur as a display movement in the Pelecaniformes. *Fregata magnificens* males spread but do not raise their tails during their rattling display. The degree of tail-spreading has not been found to be a constant feature of the other pelecaniform signal patterns that have been studied. The tail is, however, frequently spread when the tail is raised during the displays of boobies and cormorants by the "in" bird on a nest site.

Feet.

Many species of the Pelecaniformes have very colourful feet which are most vividly coloured during the breeding season. This colourfulness draws attention to the feet especially during walking, in a manner analogous to the "flashiness" of white gaiters around the ankles of
marching soldiers. This effect was also noticed during "normal" walking when coloured leg bands were placed around the black feet of crows and cormorants. It is not surprising, therefore, that Vogt (1942) used a martial term, "marking-time", to describe the stepping display of *Sula variegata*. The colour and movement of the feet apparently add emphasis to the arrival and departure displays near the nest site. This may be the origin of the stepping displays of some boobies. The lowering of the feet prior to landing may also have a signal value to the birds near the point of landing and to the mate on the nest.

Plumage.

*A. anhinga*, *Ph. carbo* and *Ph. olivaceus* have a median dorsal crest. In the Anhinga this crest occurs only in the male which raises it during the wing-waving and snap-bowing displays. The crest is only partially raised during the kink-throat display, and is depressed during the pointing display. Outside the nest the male Anhinga has his crest up unless he is alarmed, in which case the crest is lowered.

In *Ph. carbo* and *Ph. olivaceus* the median crest is up in the "out" bird and down in the "in" bird. *Ph. carbo* also lowers the median crest when alarmed (see fig. 15).

While the two median crests of *Ph. aristotelis*, *Ph. urile* and *Ph. pelagicus* are not lowered, the front crest of
Ph. aristotelis is lowered slightly during the pre-take off display.

Ph. varius raises the head and neck feathers before take off and after landing (Serventy and White 1943). Ph. melanoleucus ruffles its feathers during its wing-waving display (Harley 1946).

Several cormorant species alternately expose and cover white nuptial rump patches during the wing-waving display as was noted in Ph. carbo by Kortlandt (1938). This flashing of the rump patches is a mechanical analogue of the repetitive flashing of the mouth lining as in the darting of Ph. aristotelis, and the gaping of Ph. urile and Ph. pelagicus.

In contrast to the cormorants which have white rump patches on a black background the three species of tropicbirds have black feather patches and feet on a white background. Phaethon rubricauda during the aerial display moves its black feet towards and away from its black tertial under coverts (Udvardy unpublished MS).

Voice.

Many of the displays of the Pelecaniformes have a characteristic call associated with them. Most of these calls are species and display specific and consist of single and repetitive notes. Almost all the calls are produced vocally. The sound of the rattling display of the Fregatidae, however, is produced in part mechanically by the
mandibles rattling against each other as in the clappering displays of the White Stork, *Ciconia ciconia* (Daanje 1950, Haverschmidt 1949) and the Diomedeidae (Jameson 1958, Rice and Kenyon 1962, Richdale 1950).

As shown in table 30 for the Phalacrocoracidae the calls of a display may be either sexually distinct, or the same in both sexes, or present only in the male sex. A similar situation apparently exists in the Sulidae where the voices of *Morus bassanus* and *Sula sula* do not, and the voices of *Sula dactylatra*, *S. leucogaster*, *S. variegata*, and *S. nebouxi* do differ sexually (Dorward 1962, Murphy 1936). According to Kortlandt (1938, 1949) the voice of the female differs from that of the male only during the beginning of the breeding season, whereafter the female's voice becomes male-like.

The component parts of the communicative and non-communicative body postures, movements and sounds have, as outlined above, about two to six variants each. In combination these variants apparently are able to provide, without using all the possible combinations, the species of the Pelecaniformes with a communicatory mechanism which is able to transmit the social information necessary for successful reproduction in crowded colonies.
Table 30. Sexual Distinctiveness of Cormorant Display Sounds.

<table>
<thead>
<tr>
<th>Species</th>
<th>pre-landing</th>
<th>post-landing</th>
<th>pre-take off</th>
<th>wing-waving</th>
<th>threat</th>
<th>gape</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ph. penicillatus</td>
<td>$\delta = \varphi$</td>
<td>none</td>
<td>none</td>
<td>none</td>
<td>$\delta = \varphi$</td>
<td>$\delta = \varphi$</td>
</tr>
<tr>
<td>Ph. urile</td>
<td>$\delta = \varphi$</td>
<td>$\delta = \varphi$</td>
<td>$\delta = \varphi$</td>
<td>none</td>
<td>$\delta = \varphi$</td>
<td>$\delta \neq \varphi$</td>
</tr>
<tr>
<td>Ph. pelagicus</td>
<td>$\delta = \varphi$</td>
<td>$\delta = \varphi$</td>
<td>$\delta = \varphi$</td>
<td>none</td>
<td>$\delta = \varphi$</td>
<td>$\delta \neq \varphi$</td>
</tr>
<tr>
<td>Ph. aristotelis</td>
<td>only</td>
<td>only</td>
<td>only</td>
<td>none</td>
<td>only</td>
<td>only</td>
</tr>
<tr>
<td>Ph. auritus</td>
<td>$\delta = \varphi$</td>
<td>$\delta = \varphi$</td>
<td>$\delta = \varphi$</td>
<td>only</td>
<td>$\delta = \varphi$</td>
<td>$\delta = \varphi$</td>
</tr>
<tr>
<td>Ph. carbo</td>
<td>$\delta \neq \varphi$</td>
<td>$\delta \neq \varphi$</td>
<td>$\delta = \varphi$</td>
<td>none</td>
<td>$\delta \neq \varphi$</td>
<td>$\delta \neq \varphi$</td>
</tr>
</tbody>
</table>

Key:
$\delta = \varphi$ ..... male and female calls the same
$\delta \neq \varphi$ ..... male and female calls differ
$\delta$ only ..... only male calls
none ..... no calls made
? ? ? ..... not known
Function of communication patterns.

As mentioned in the introduction the actual amount of information that is passed from one animal to another cannot be determined without experimentation. An approximate estimate, however, can be made of the potential information content of displays and of the basic minimum of information that has to pass between animals before the observed reactions and cooperations between them can occur.

By analyzing the information that has to be passed between two pelecaniform birds so that they may form a pair and successfully raise their brood and by reviewing the potential information inherent in their displays it is possible to postulate at least part of the most likely communicatory functions of these displays. The assumption is then made that these birds can perceive the information that the human observer and his instruments can obtain from their displays.

In the Pelecaniformes as in many other bird species it is the male that takes the initiative during courtship. He selects the nest site and on it advertises the fact that he is a male, single, and owns a potential nest. This advertising is done in the American White Pelican by the masculine form of the reach-bowing, in gannets by the masculine form (?) of head-wagging and wing-bowing, in boobies by sky-pointing, in anhingas by wing-waving, in cormorants by wing-waving, in the Shag by darting and the
throw-back, and in frigatebirds by the masculine form of rattling. In the tropicbirds the male-advertising probably takes place in the air after which the male guides the female to the nest cavity.

Once a female responds to the advertising of a male he indicates whether he is prepared to tolerate her as a potential mate at the nest site. If she is not acceptable to the male she is chased away with threats and bites. If necessary the male removes her forcibly from the nest. Females react to this passively and have not been observed then to threaten or fight back at a male. If she is acceptable the males of some species such as the American White Pelican, gannets and frigatebirds, continue to use the same display as they used for advertising as a recognition display, after the female arrives at the nest site. The sky-pointing of boobies, and the wing-waving of anhingas and cormorants cease when a female visits the nest site. The male then switches to one of the various recognition displays of these species such as nest-worrying, head-throwing, gaping, bowing, etc. These recognition displays are continued by both the male and the female as long as the pair remain together.

The sky pointing and wing-waving normally cease after there are eggs in the nest. According to Murphy (1936) the "gular sac" of the male frigatebird is not inflated when there are eggs in the nest.
The Pelecaniformes do not have any distinctive alarm calls although they do react to the alarm calls of the crows and gulls that are present in their colonies. When they are alarmed pelicans, gannets, boobies, anhingas, and cormorants raise their heads with their bills tilted slightly upwards and flatten their plumage. Next they fly away silently without any take off display. The pre-take off display of gannets, boobies, anhingas and cormorants may, therefore, serve to signal that a bird is leaving for some reason other than that it has been frightened away. This may help to encourage the birds on nest guard to remain where they are and thus help to protect the progeny in the nest.

The pre-landing and post-landing displays of the Pelecaniformes may help to announce the arrival back of the nest and thus help the bird on the nest to distinguish its mate from any conspecifics approaching the nest.

The pelecaniform birds probably recognize their own species mainly by the colour patterns and crest patterns of the head and upper neck, plus the colour of the mouth lining. Behavioural species-specific clues are the wing posture during sky-pointing in the gannets, post-landing postures and gape-displays in the cormorants, and the voices of cormorants and tropicbirds. The wing-waving of cormorants is species-specific in some sympatric species but not in *Ph. auritus* and *Ph. olivaceus* in Louisiana, and *Ph. urile* and *Ph. pelagicus* in the Aleutian Islands of Alaska.

Sex recognition is probably no problem to
species like the anhingas and frigatebirds which differ sexually in colour, the pelicans which differ sexually in size, and some of the boobies and cormorants which differ sexually in the sounds they make during some of their displays. In the boobies, anhingas, and cormorants the sky-pointing and wing-waving signal malesness during the courting period. In some species such as the American White Pelican, the Great Cormorant, and the Magnificent Frigatebird the movements of the recognition displays are sexually distinct.

How the gannets and tropicbirds are able to recognize the sex of conspecifics is still an unsolved problem. It is possible that the gannet can perceive a sexual difference in the head-wagging and wing-bowing displays. It may well be, however, that a single female gannet approaches each single gannet displaying on its nest irrespective of it being a male or female calling for its mate, and that eventually after many rejections she is accepted by a single male who recognizes her as a female because she does not actively resist any of his threats. In the tropicbirds it is probably that it is the male that is upper most during the aerial displays, but this has not yet been demonstrated.

Possible communicatory mechanisms have been found in the Pelecaniformes, which are potentially able to alert,
attract and repel conspecifics, and to transmit species, sex and individual identity. Further study and experimentation should be able to establish the full information content of these signals.
Phylogeny of communication patterns.

The attributes of the communicatory mechanisms of a species are, like those of its anatomy and physiology, subject to the forces of natural selection. This selection should tend to favour increases in the distinctiveness and the information content of a signal. Each signal posture and movement should differ from all other postures and movements, with and without signal value to the same animal. An ideal signal should be individually, sexually, and species-specifically distinct. Consequently there should be selective forces operating on the social communication patterns which promote: individual consistency, intra-sexual and intra-specific consistency and divergency, and inter-sexual and sympatric inter-specific divergency.

The various threat, recognition and male-advertising displays of the Pelecaniformes seem to have been derived from one or more of four major sources: locomotion, fighting, nest-building, and begging - as is outlined in the descriptive sections and in figures 41, 42, 43 & 44 respectively and will be further discussed below.
Pre-take off derivatives (fig. 41).

The sky-pointing display of the boobies appears to have derived its vertical bill, head, and neck posture from the look phase, and its horizontal body posture from the crouch phase of the pre-take off display of the gannets. The backward rotation of the wings seems also to be a pre-take off derivative, while the call note of the sky-pointing is probably related to the post-take off and hop call of gannets. The upward posture of the tail may have come from one of the other displays of boobies such as the bowing.

The pathway which transformed a pre-take off display into a male-advertising display may have been the transfer of the nest site from the male to the female during courtship. By ritualization the departure was first slowed down to a pre-take off display, next reduced to a hop and finally to a token pre-departure signal without the feet leaving the ground. Subsequently, if not at the same time, the true pre-departure signal and the derived signal diverged in form thus improving the conveyance of their respective meanings. Thus the pre-take off of the boobies lacks the gannet's vertical bill posture and backward rotation of the wings, which have been retained in the sky-pointing of the boobies. The hop of *Sula sula* is silent, whereas that of the gannets is vocal. A similar
process probably took place during the evolution of the stretch display of the herons (Meyerriecks 1960, Verwey 1930).

The sky-pointing diverged species-specifically in the boobies in the extent the wings move apart during the display, with only the allopatric *Sula nebouxii* and *S. variegata* having the same variant of the display.

From the boobies the sky-pointing has evolved into the wing-waving displays of the anhingas and cormorants with a retention of its male-advertising function. In the anhingas and cormorants the vertical posture of the neck, head and bill which occurs in the sky-pointing of the boobies has been lost. The wing movement is repetitive in the Anhinga and most cormorant species and not single as in the boobies. This wing movement is alternate in the Anhinga and simultaneous in the cormorants except for the Shag. In some cormorants the head moves down onto the back as the wing tips move up. While the Shag has lost the wing component of the display it has retained the body posture and the head movement in its throw-back display. In this species a threat derivative, the darting, has taken over some of initial female-attracting functions of the male-advertising display from the wing-waving and its derivative, the throw-back. In some cormorant species the flashing of white rump patches takes the place of the call notes that accompany the raising of the wing tips in boobies and some other cormorant species. In the little Pied Cormorant, *Phalacrocorax melanoleucus*, there is a
switohing back and forth between the body postures of the look and the crouch phases of the pre-take off displays in a manner analogous to the stretch display of herons. Whether \this is a primary or a secondary phenomenon only further study will tell.
Fig. 41. Phylogenetic Tree of Pre-take off Derivatives.
Threat derivatives (fig. 42).

How a threat may evolve from fighting and into a recognition display has been explained in the descriptive part of the text. Here as in the evolution in function from the pre-take off to the male-advertising in the sky-pointing, the threat and the threat-derived recognition display have diverged in form. Thus the head-raising of pelicans and the head-throwing of the Red-footed Boobies lack the gape component of the threat displays of these and other pelecaniform species. In the cormorants it is the gape component that is common to their threat and their gape displays and it is the head and neck postures and movements that differ. Head-raising and threat in the pelicans have a common raising of the bill tip, while the head and neck movements hardly differ between the threat and head-throwing displays of the Red-footed Booby.

Vocal differences have evolved between the threat and the gape displays of some of the cormorants. Like the wing-waving the gape display has become repetitive in some cormorant species. In addition to the gape display threat has given rise to the darting display in the Shag.

The derivation of the pointing displays of anhingas and some cormorants is still an unsolved problem. The pointing lacks sound and movement and can structurally be just as easily regarded as a derivative of the sky-pointing of boobies as of the gaping of the Double-crested and Olivaceous Cormorants.
Figure 42. Phylogenetic Tree of Threat Derivatives.
Nest-building derivatives (fig. 43).

As has been mentioned in the section on defensive nest-indicating, the act of "handling" nest material may indicate to other birds that a bird is sitting on a nest site and is prepared to defend more than only perching space and its individual distance. Thus the nest-worrying of cormorants may serve a defensive threat function and indicate to a potential mate the ownership of a nest site. Thus the bowing postures of pelicans, gannets, boobies, anhingas, and some cormorants may have evolved with a reduction of movement from the nest-building movements. In the American White Pelican two bowing movements appear to have evolved independently, the reach-bowing from the reaching for nest material and the wave-bowing from the worrying of nest material.

In the Red-footed Booby the front-bowing follows often immediately after the sky-pointing and sometimes retains the raised condition of the wing tips of the latter display. This may be how the snap-bowing of the Anhinga acquired the simultaneous raising of the wings, which in turn may have caused the wing-waving of this species to become an alternating movement of the wings for contrast.

The change of body posture in the gape-bow of the Little Pied Cormorant is analogous to that in the snap display of the herons (Baerends & van der Cingel 1962, Verwey 1930), and would merit further study.
Snap-bowing
A. anhinga

Front-bowing
S. sula

Front-bowing
Ph. aristotelis

Quiver-bowing
S. leucogaster
S. dactylatra

Wave-bowing
P. erythrorhynchos

Reach-bowing
P. erythrorhynchos
P. occidentalis

WING-WAVING

Gape-bowing
Ph. melanoleucus

Side-bowing
S. leucogaster
S. dactylatra

Wing-bowing
M. bassanus
M. capensis
M. serrator

NEST-WORRYING

NeST-BUILDING

Figure 43. Phylogenetic Tree of Nest-building Derivatives.
Food-begging and its derivatives (fig. 44).

How food-begging may have evolved into an adult courtship pattern has been outlined in the descriptive part of the text. Food-begging has given rise to a pre-landing display in probably all the Pelecaniformes. In the gannets, boobies, anhingas, cormorants and frigatebirds food-begging derivatives are associated with the bringing and receiving of nest material. The food-begging derivatives retain in each family the characteristics of food-begging of that family, for example the tail-spread in the frigatebirds and the forward movement of the hyoid apparatus in the anhingas and cormorants.

In the gannets both members of a pair head-wag facing each other on the nest site. This may have led to the frigatebirds rattling side by side facing opposite directions on their smaller arboreal nests.

The extreme sideways swing of the head-wagging of the Red-footed Booby may have evolved from a fusion of the alternative head-wagging and wing-bowing of the gannets.

As outlined above the displays of the pelecaniformes have diverged in form and function within species and between species.
Figure 44. Phylogenetic Tree of Food-begging Derivatives.
Fig. 45. Phylogenetic Tree of the Pelecaniformes adapted from Lanham (1947).
Figure 46. Phylogenetic Tree of the Pelecaniformes. Species studied are listed. Solid lines indicate reasonably certain relationships. Dashed lines indicate possible relationships. Adapted from Sibley (1960).
Fig. 47. Some Common Social Attributes (horizontal lines) of Pelecaniform Genera (vertical lines).
Fig. 48. Some Common Social Attributes (horizontal lines) of Sulid Species (vertical lines).
<table>
<thead>
<tr>
<th>Ph. varius</th>
<th>Ph. auritus</th>
<th>Ph. olivaceus</th>
<th>Ph. carbo</th>
<th>Ph. penicillatus</th>
<th>Ph. pelagicus</th>
<th>Ph. urile</th>
<th>Ph. aristotelis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gaping</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>repetitive</td>
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</tr>
<tr>
<td>neck stretched</td>
<td>Median Crest raising</td>
<td>Wing-waving</td>
<td>Slow rate</td>
<td>Pre-hop</td>
<td>neck not arched</td>
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<td></td>
<td></td>
<td></td>
<td>rapid flutter</td>
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<td></td>
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</tr>
<tr>
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<td>pointing</td>
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<tr>
<td>Gaping</td>
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<tr>
<td>Kink-throating</td>
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</tr>
<tr>
<td>Repetitive Wing-waving</td>
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</tr>
</tbody>
</table>

**Fig. 49.** Some Common Social Attributes (Horizontal lines) of Phalacrocoracid Species (Horizontal lines).
Phylogeny of the Pelecaniformes.

The order Pelecaniformes has been recognized as a distinct taxonomic entity, the Totipalmes by Cuvier in 1805, and the Steganopodes by Illiger in 1811 (Gadow 1893). Even now it is one of the few orders that Mayr and Amadon (1951), Stresemann (1927-1934, 1959), and Wetmore (1951) agree on in their respective systems of avian classification.

The living pelecaniform birds are divided into five families by Berlioz (1950b), Dementiev and Gladkov (1951), Mayr and Amadon (1951), Sibley (1960), and Stresemann (1927-1934), and into six families by Lanham (1947), Peters (1951), Storer (1960), and von Boetticher (1957). The discrepancy is due to the question whether the Anhingidae are a family, or a sub-family, the Anhinginae of the Phalacrocoracidae. Sibley (1960) recommends that the monotypic genus Anhinga should be placed in the same sub-family as Phalacrocorax.

Lanham (1947), Peters (1931), von Boetticher (1957), and Storer (1960) combine the Sulidae, Phalacrocoracidae, and the Anhingidae into the super-family Suloidea, and add the Pelecanidae to these three families to form the sub-order Pelecani. They place the Fregatidae and the Phaëthonidae into separate sub-orders, the Fregatae and the Phaëthones (fig. 45).

Lanham (1947) presents anatomical, and Sibley (1960) egg-white electrophoretic, data that the Fregatidae
and the Phaethontidae are more closely related to each other, than either of them to the Pelecani (figs. 45, 46).

Lanham (1947) considers the Anhingidae and the Phalacrocoracidae on the basis of their anatomy to be the most closely related pelecaniform families. On the basis of *Protoplotus* Lambrecht, he estimates that the anhingas diverged from the cormorants during the Eocene. Sibley (1960) found the egg-white proteins of anhingas and cormorants to be virtually identical. This similarity contrasts with the vast differences between the egg-white proteins of *Morus bassanus*, *Sula sula* and *Sula dactylatra*.

By using the attributes of the social behaviour of the Pelecaniformes which its genera and species have in common, figures 47, 48 and 49 have been drawn following the method of Lorenz (1941). In the figures the vertical lines represent either genera or species and the horizontal connecting lines common attributes. These diagrams tend to support the phylogenetic tree of Lanham (fig. 45) more than the tree of Sibley (fig. 46). This difference as well as other differences in the classification of the Pelecaniformes are discussed below in the light of their behavioural attributes for each taxon.
Order Pelecaniformes.

The close affinites of the Pelecaniformes to Procellariiformes and the Ciconiiformes are indicated by the mutual displaying of members of a pair facing each other on the nest site as occurs not only in the gannets and in a modified form in the frigatebirds but also in the albatrosses, fulmars and storks. A further resemblance can be noted as mentioned earlier in the text between the rattling of frigatebirds and the clappering displays of albatrosses and storks, between the stretch display of herons and the sky-pointing of boobies and the wing-waving of the Little Pied Cormorant, and between the snap display of herons and the snap-bowing of the Anhinga and the gape-bowing of the Little Pied Cormorant. How many of these similarities are due to either homology or analogy still remains to be studied.

The pelecaniform birds have in common a similar method of feeding their young and a similar pre-landing display which appears to be a food-begging derivative.
Sub-order Phaethontes.

The tropicbirds differ from the other pelecaniform birds in their lack of any nest-building behaviour. The three tropicbird species are almost identical in their aerial displays which resemble the pre-landing displays of the other pelecaniform birds.

The social behaviour of the tropicbirds at their nest except for inter- and intra-specific agonistic behaviour (Stonehouse 1962b) is almost totally unknown and should merit further study.

Sub-order Fregatae.

The frigatebirds have in common the red balloon-like "gular sac" of the males which is very prominent during their rattling display. This display resembles the pre-landing display of other pelecaniform birds and the food-begging of the frigatebird chicks. The frigatebird species appear to be almost identical in their feeding and social behaviour.

Sub-order Pelecani.

The pelicans, gannets, boobies, anhingas, and cormorants use not only food-begging derivatives but also nest-building derivatives such as the various bowing
displays as social signals. These birds unlike the frigate-birds and tropicbirds are able to walk to, from, and around, their nest sites which faculty gives them greater freedom to express themselves.

Super-family Pelecanoidea,

The social behaviour of most pelican species is totally unknown. The four species that have been partially studied have in common the bill-raising display. In this display as well as the aerial, reach-bowing, and wave-bowing displays of *Pelecanus erythrorhynchos* the expansion of the huge gular pouch of the pelecanids plays a major role. It is very probable that the social displays of the other pelican species which are mostly allopatric will be found to be very similar to those of the American White Pelican.

Super-family Sulcoidea.

The gannets, boobies, anhingas, and cormorants have in common the performance of pre-take off and post-landing displays and the combination of these displays into hop displays. The origin of the male-advertising displays, sky-pointing and wing-waving of the boobies, anhingas and cormorants can be traced back to the pre-take off displays of gannets. Thus the Sulidae are more closely related to the Anhingidae and Phalacrocoracidae than to the Pelecanidae
as is suggested by the current classifications and the phylogenetic tree of Lanham (fig. 45) but not of Sibley (fig. 46).

Super-family Sulidae.

The gannets and boobies resemble each other in their feeding habits and external appearance. They differ markedly, however, in the form and functions of their various social signals. Whereas the gannets tend to display opposite each other as mirror images as in albatrosses, fulmars, and storks, there is in the boobies a clear difference in behaviour and posture between the "in" bird and the "out" bird as occurs in anhingas and cormorants. The gannets do not have the sky-pointing as a male-advertising display as is the case in the booby species that have been studied. This supports the placing of the gannets and boobies into two separate genera, Morus and Sula as is done in the A.O.U. Checklist (1957) and by Alexander (1955, 1959), Berlioiz (1950a), Murphy (1936), Palmer (1962), Peterson (1960), Jorgenson (1958) and von Boetticher (1957), but not in the B.O.U. Checklist (1952), and by Fisher (1947), Peterson et al (1954), and Sibley (1960).
Family Anhingidae.

The Anhinga, though closely resembling the cormorants in its kink-throat and pointing displays, and both the boobies and cormorants in its wing-waving and bowing displays, is distinctive enough in the latter two displays to merit remaining in a separate family, the Anhingidae, and not to be placed in a sub-family, the Anhinginae of the Phalacrocoracidae. Although it is likely that the anhingas and cormorants diverged after evolving from booby-like stock as is indicated by the sky-pointing and wing-waving displays, the differences in the studied behaviour patterns between the anhingas and cormorants are now of the same order of magnitude as between either of them and the boobies.

Family Phalacrocoracidae.

The cormorants differ from the other pelecaniform birds in their wing-waving and gape displays. The wing-waving of cormorants is, however, related to the wing-waving of anhingas and the sky-pointing of the boobies. The gape display of cormorants is related to the head-throwing of the Red-footed Booby.

The genus Phalacrocorax has about as many living species in it (28 species) as there are in all the other
extant pelecaniform genera (26 species). The social signals of only seven cormorant species were observed during this study and only fragmentary data is available in the literature on the signals of some of the other cormorant species. Nevertheless a tentative division can be made between the cormorants with a continental distribution such as Ph. carbo (Old World), Ph. auritus (North America), Ph. olivaceus (South America) and those with a marine coastal distribution Ph. aristotelis (N.E. Atlantic), Ph. urile (Bering Sea), Ph. pelagicus (North Pacific), and Ph. penicillatus (N.E. Pacific).

The continental cormorants differ from the marine cormorants in their ability to perch in trees, include sticks in their nest material, make shallow as well as jump dives, in the heron-like posture of their necks during flying, and a wing-waving rate about half the speed of the marine cormorants.

The marine cormorants differ from the continental cormorants by arching their necks before hopping, by flying with their necks either stretched forward like a crane (Ph. aristotelis, Ph. urile, and Ph. pelagicus) or with their necks depressed like a loon (Ph. penicillatus). In Ph. aristotelis the head moves up and down in the throw-back display at about the same rate as both the head and the wing tips move up and down in the wing-waving of the other three marine cormorants that have been studied.

A very close resemblance was found within the species pairs Ph. urile and Ph. pelagicus, and Ph. auritus
and *Ph. olivaceus*. Behaviourally the first pair differs in both the pre-take off and post-landing displays, while the latter pair differ only in their post-landing displays. Each pair has its own characteristic gaping display and the first pair has a unique twisted body method of take-off.

The switching of the body posture in the wing-waving and gape-bowing displays of the Little Pied Cormorant, *Ph. melanoleucus*, might be a characteristic of the sub-genus *Haliéter* Heine. This sub-genus consists of the four micro-cormorant species, *Ph. africanus*, *Ph. pygmeus*, *Ph. niger*, and *Ph. melanoleucus*, which have an inland as well as marine allopatric distribution forming a crescent around the Indian Ocean from South Africa to New Zealand. Some authors consider *Haliéter* to be a separate genus (Alexander 1955, 1959, Peters 1931, and von Boetticher 1957) while others (Berlioz 1950a, Jorgensen 1958, and Peterson et al 1954) include it in the genus *Phalacrocorax*. Only further study will determine the correct status of the micro-cormorants.
Conclusions.

The social communication patterns of the Pelecaniformes consist of various combinations of a limited number of postures, movements, and calls. These combinations are sufficiently consistent within each taxon to reflect their phylogenetic histories.

The evolution of some displays can be deduced from their present forms in a group of related species. Other displays show a complete gradation from derivation to the derivative within a single species. In their divergence from their origin the signals have become less irregular and more distinctive, and have changed in form and function.

While some displays have in some species become either sexually or positionally different, they have not done so in related species. Advertising displays have become restricted to the male sex, but apparently none have become restricted to the female sex.

The signals of too few species have been studied in sufficient detail for these signals to form a basis for a revision of the current classifications of the Pelecaniformes. However, the phylogenetic implications of these classifications help to explain, and are supported by, the behavioural data that are available.
Summary.

1) A comparative study was made of social communication patterns of *Pelecanus erythrorhynchos*, *P.onocrotalus*, *P.crispus*, *P.occidentalis*, *Morus bassanus*, *Sula sula*, *Anhinga anhinga*, *Phalacrocorax carbo*, *Ph.auritus*, *Ph.olivaceus*, *Ph.aristotelis*, *Ph.urile*, *Ph.pelagicus*, *Ph.penicillatus*, and *Fregata magnificens*.

2) It was found that the signal patterns are combinations of a limited number of discrete postures, movements, and sounds, and that they are mainly derivatives from four main sources, locomotion, fighting, nest-building, and begging.

3) The take-off was found to consist of three phases, look, crouch, and leap. From the look and crouch phases the Suloidea have evolved their pre-take off displays, while from the recovery after landing they have evolved their post-landing displays. The pre-take off and post-landing displays are combined into a hop display in this super-family.

4) The sky-pointing, a male-advertising display of *Sula*, is a derivative of the pre-take off display of *Morus*, and is the origin of the wing-waving as a male-advertising display in *Anhinga* and *Phalacrocorax*. The second part of the male-advertising display of *Phalacrocorax aristotelis*, the throw-back, is a derivative of the wing-waving displays of the other cormorants.
5) Threat displays have evolved into recognition displays in the bill-raising of the Pelecanidae, the head-throwing of *Sula sula*, the gaping of the Phalacrocoracidae, and into the first part of the male-advertising display of *Phalacrocorax aristotelis*, the darting.

6) Nest-indicating displays have evolved from the reaching for nest-material into the reach-bowing of *Pelecanus erythrorhynchos*, and from nest-worrying movements into the wave-bowing of *P. erythrorhynchos*, the wing-bowing of *Morus*, the front-bowing of *Sula sula*, the quiver-bowing of *S. leucogaster* and *S. dactylatra*, the snap-bowing of *Anhinga anhinga*, the front-bowing of *Ph. aristotelis* and the gape-bowing of *Ph. melanoleucus*.

7) The food-begging of the chicks has evolved in the adults into the aerial display of *Pelecanus erythrorhynchos*, the head-wagging of the Sulidae, the kink-throating of the Anhingidae and the Phalacrocoracidae, the rattling of the Fregatidae, and the aerial displays of the Phaethontidae.

8) From a comparison of the taxonomic distribution of the form, function, and derivation of the social communication patterns in the Pelecaniformes, it was concluded that they reflect the phylogenetic implications of the current systematic classifications of the order.
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