

**Association Patterns and Pod Cohesion
in Northern Resident Killer Whales (*Orcinus orca*)**

by

Elvira Harms
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Department of Zoology

The University of British Columbia
Vancouver, Canada

Date 28.4.97

ABSTRACT

Understanding the social structure of a killer whale community may give insight into the short-term factors that determine pod-cohesion and pod-splitting. Social patterns within British Columbia's northern resident killer whale community were analyzed using a 20-year long photographic database. Females were found to associate primarily with their mothers when young, and with their own offspring later in life. They showed a surprising lack of contact with other females in their pod, and were photographed more often with females of other pods. Males seemed to be the preferred associates of all pod members, especially other males. Upon reaching age 21, males showed an explosion in social contacts of all sorts, especially with their extended kin.

The results suggest that it is male social bonds that give cohesion to killer whale pods, binding two or more related female-offspring units. Female associations are mainly between mothers and their offspring, and their associations with females of other pods may give some cohesion to the community as a whole. These patterns lead to the prediction that without an adult male and the possibility of male-male bonds between mother-offspring units, a pod is likely to split after the death of the common mother. This prediction is consistent with observed cases of pod-splitting.

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INTRODUCTION

Dispersal is common in the animal kingdom but it seems to be rare among the resident killer whales (*Orcinus orca*) of British Columbia and Washington State. In almost two decades of observation, individual dispersal has not been observed in B. C. resident killer whales, although a few cases of pod splitting have been reported (Bigg et al. 1990, Ford, pers. comm.). Thus, dispersal in resident killer whales seems to occur at the level of the group rather than at the individual level. Understanding pod cohesion, or pod splitting, requires comprehension of the factors that bind a pod together. Factors potentially affecting pod cohesion include evolutionary, ecological, and social factors.

Female killer whales produce only 5-6 viable calves in their lifetime, but are receptive sexually up to eight times per year (Olesiuk et al. 1990; Walker et al. 1988). It may be important therefore for males to stay with females so they do not miss mating opportunities. It is also known that pod members are highly related to each other matrilineally. This means that any potential advantages or disadvantages of inbreeding are relevant to killer whale society. There is a substantial literature premised on the need for inbreeding avoidance (Greenwood, 1980; Pusey and Packer, 1987), as well as arguments against the universality of inbreeding avoidance (Shields 1982; Chepko-Sade 1987; Moore and Ali 1984). Bain (1989) discussed the costs and benefits of brother coalitions for ensuring mate access in killer whales, and the genetic advantage to restricting outbreeding. But the mating pattern in killer whales is not yet known. The DNA studies that will provide valuable information in this regard are currently in progress at the University of British Columbia (pers. comm. Barrett-Lennard, 1997).

Since killer whales have no natural predators, predation avoidance is not a reason for or against staying in groups. Communal defense of ephemeral food resources such as fish also seems an unlikely explanation, and there is no evidence to suggest that it occurs. However, ecological constraints on hunting strategies may influence pod size. Larger groups may be more efficient for hunting some types of prey under some conditions, or groups may become too large for hunting efficiency, or for local carrying capacities (Ford 1991; Olesiuk et al., 1990; Baird and Dill, 1996).

Killer whales are highly social and intelligent animals, so it is reasonable to expect that social bonds would be important proximate determinants of group cohesion. Even if the ultimate reasons for pod cohesion and splitting are long term and external (e. g. ecological or evolutionary), the proximate causes may be perceivable in the constraints and dynamics of killer whale social systems.

This thesis examines the social structure of the northern resident killer whales of British Columbia using the large and long-term photo identification dataset started by Michael Bigg in 1973 (Bigg et al. 1987).

Study species

Along the coast of British Columbia and Washington State, there are two forms of killer whales known as 'residents' and 'transients' (Bigg et al. 1987). The two forms are sympatric but do not associate, and they differ in feeding behaviour, morphology, dialect and social organization (Balcomb et al. 1982; Bigg 1982; Bigg et al. 1987; Bain 1988; Ford 1987, 1990; J. Heimlich-Boran, 1986; S. Heimlich-Boran 1986, 1988; Olesiuk et al. 1990).

Transients feed mainly on marine mammals, use less echolocation, tend to travel in smaller groups (2-10 individuals), and have been observed to disperse (Bigg et al. 1990; Barrett-Lennard et al. 1996; Baird and Dill 1996). Residents are mainly piscivorous, relatively vocal, and travel in stable matrilineal groups or pods of 5 to 40 individuals (Bigg et al. 1990). Two main populations make up the resident community, distinguished by their separate geographical home ranges: northern and southern. Although the home ranges of these populations overlap, members of the two populations have not been seen together. This study examines only the northern resident community, because it is the larger of the two resident communities, and was less affected demographically and socially by live capture for aquariums in the 1960s. Finally, almost all individuals from this population have been identified and catalogued on the basis of natural markings and fin shape (Bigg et al. 1987).

Killer whale kin groups are hierarchies of progressively inclusive matrilineal units (MLUs), which consist of a mother and her offspring (Bigg et al. 1990). Resident killer whale offspring stay with their mothers throughout life. Subpods and pods are defined according to the proportion of time their members are seen together. Bigg et al. (1990) define subpod (s) as "matrilineal group(s) that almost always (> 95 % of the time) travel with one another"; and pods as "subpod(s) that travel with one another the majority of the time".

The Data

The dataset available to me consisted of several thousand records, collected and recorded from 1973 to present, by the late Mike Bigg and coworkers, and archived at the

Pacific Biological Station, Department of Fisheries and Oceans, Nanaimo, B. C. I refer to it here as the "Bigg dataset" or "Bigg database". Much has been learned from this dataset about the northern community, such as its demography, genealogy (Bigg et al. 1990; confirmed by Bain, 1988), and fecundity (Bigg et al. 1990; Olesiuk et al. 1990).

ANALYSIS & RESULTS

This study is an exploratory data analysis in which methods and results are intertwined. They will be dealt with together in this section. I used AWK, a powerful and flexible data manipulation language (Aho et al. 1988), to check and prepare the database for my analysis. For graphical output I used Splus (Becker et al. 1988). My exploration began with refining the Bigg database, checking for bias, and then subsetting to avoid possible sources of error.

Data preparation

Each record of Bigg's dataset was derived from a separate photograph, and had the following fields: date, encounter number, photographer, location, number of film roll, number of frame, visual entry, photo ID's of the whales, and comments. I transcribed five years of data (1988 to 1992) from the log sheets into the computer database, and brought it to its most complete form. I corrected all inconsistencies in case and spelling and removed records with nonsense whale ID's that could not be corrected.

Almost all of the whales in the photographs were identified by three people only (Bigg, Ellis and Ford), who came to know the whales best over the years, and also took the vast majority of the photographs. This probably implies that accuracy and sampling method were fairly constant. The photos were taken to determine whale identities, rather than to study whale associations or social structure. On one hand, this means that the data were collected without assumptions about social structure. On the other hand, biases may exist due to efforts to solve identification problems, e.g. photographs taken during rest rather than play.

Checking for biases

The photographs were not taken randomly. They were collected for the purpose of identifying each whale encountered on a particular day (Bigg et al. 1987). Usually the sequence consisted of a methodical sweep through the pod. Multiple pictures taken of the same whale(s) were unavoidable, and some may be intentional "insurance" photos because of harsh weather conditions. I deleted consecutive frames containing the same whale(s) from the database.

I inspected the data visually for general patterns that might have had implications for my analysis. First the sampling intensity over time, as measured by the number of film rolls taken, was plotted by year (Figure 1) and by season (Figure 2). Sample effort in each year showed little overall variation among years, although the fewest photos were taken in 1976 and 1977 (Figure 1). However, almost 75% of the pictures were taken in the summer months July and August (373 and 493 film rolls respectively, out of 1177; Figure 2). July through September is the period during which the orcas gather in Johnstone Strait and feed on migrating salmon (Nichol et al. 1996). I decided to continue the analysis with only those three months' records to avoid possible biases from seasonal changes in social structure.

Next, to check for any over or under represented pods, the number of film rolls containing photos of any pod's member(s) was determined for each year. Figure 3 shows medians and the variation in yearly pod sightings. Pod A01 was the most frequently photographed pod during the summer months. None of the pods were taken out since I assumed some generality to the social structure of a pod.

Figure 1. Number of film rolls taken by year, in the Bigg database.

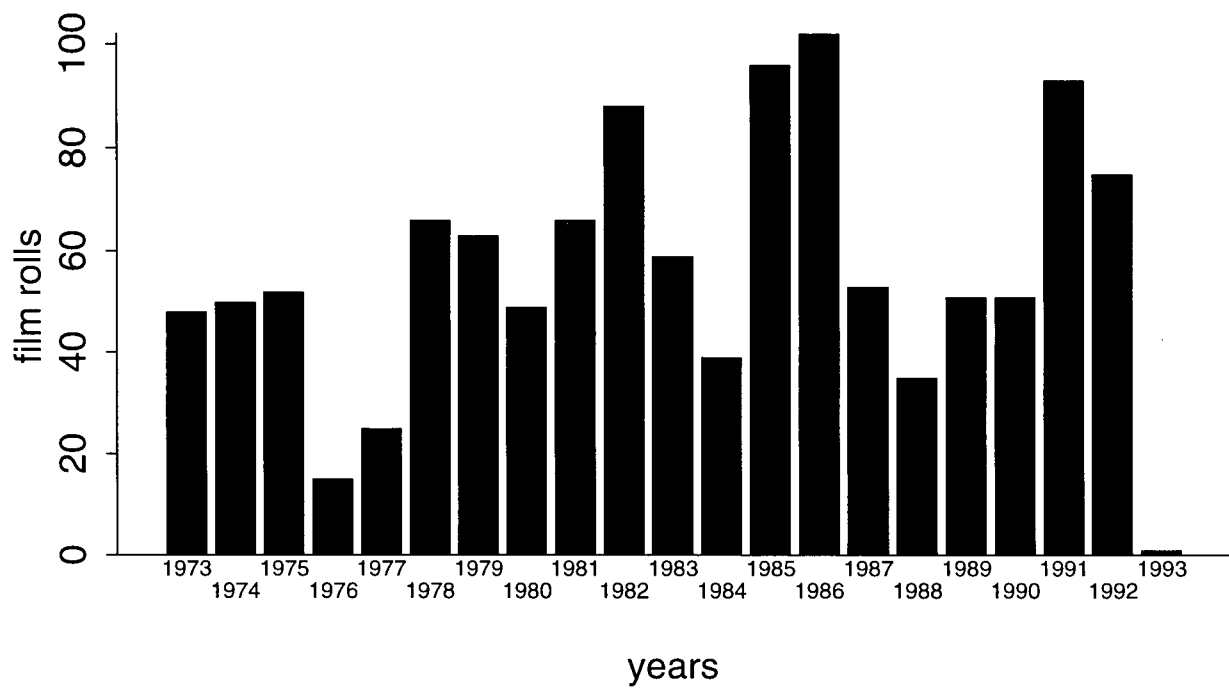


Figure 2. Number of film rolls taken by month, in the Bigg database.

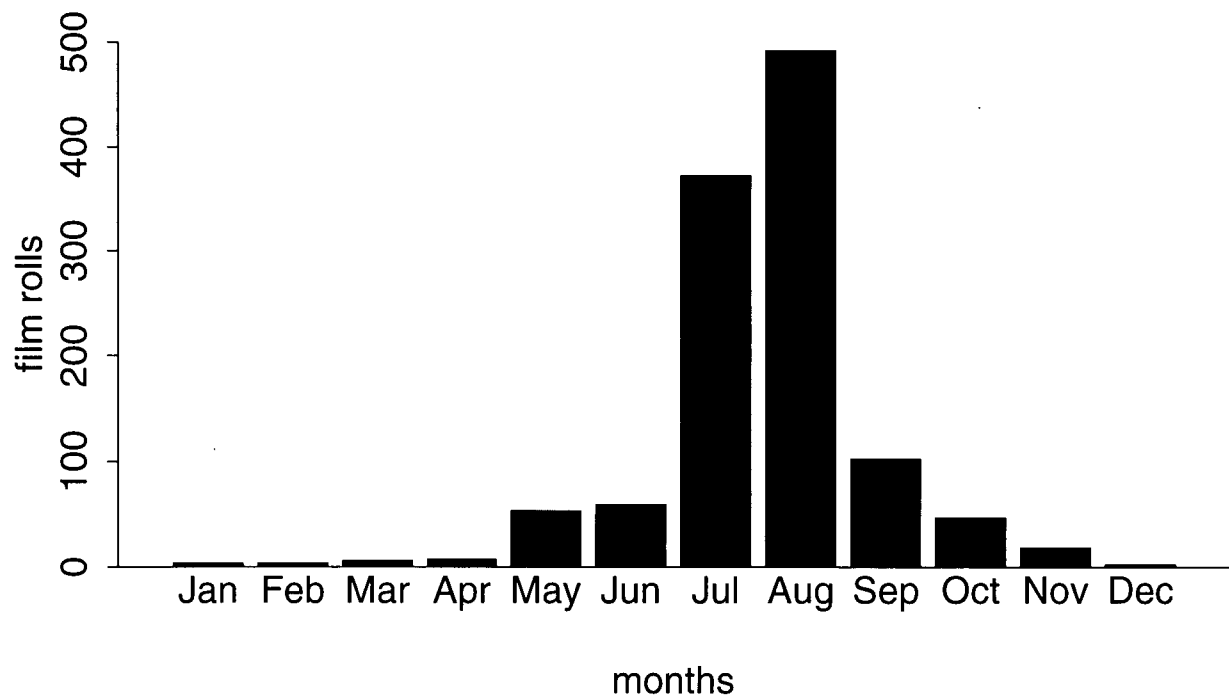
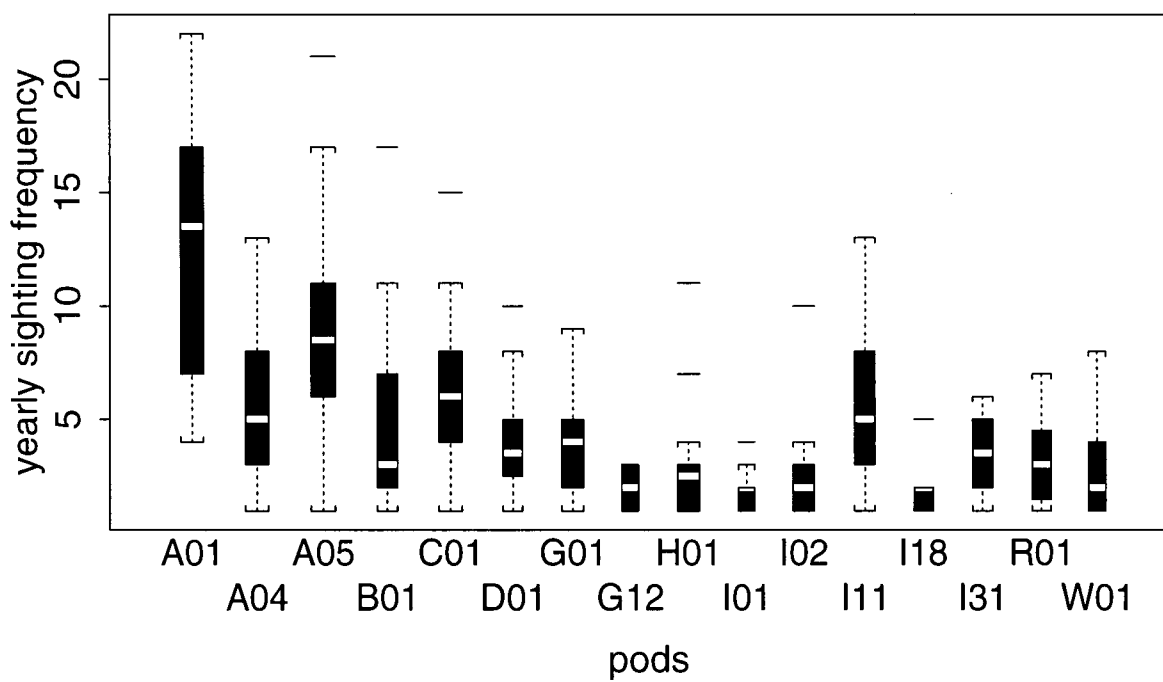


Figure 3. Yearly sighting frequencies of each northern resident pod in the Bigg database.
(The central white bar is the median, surrounded by the central quartiles.)

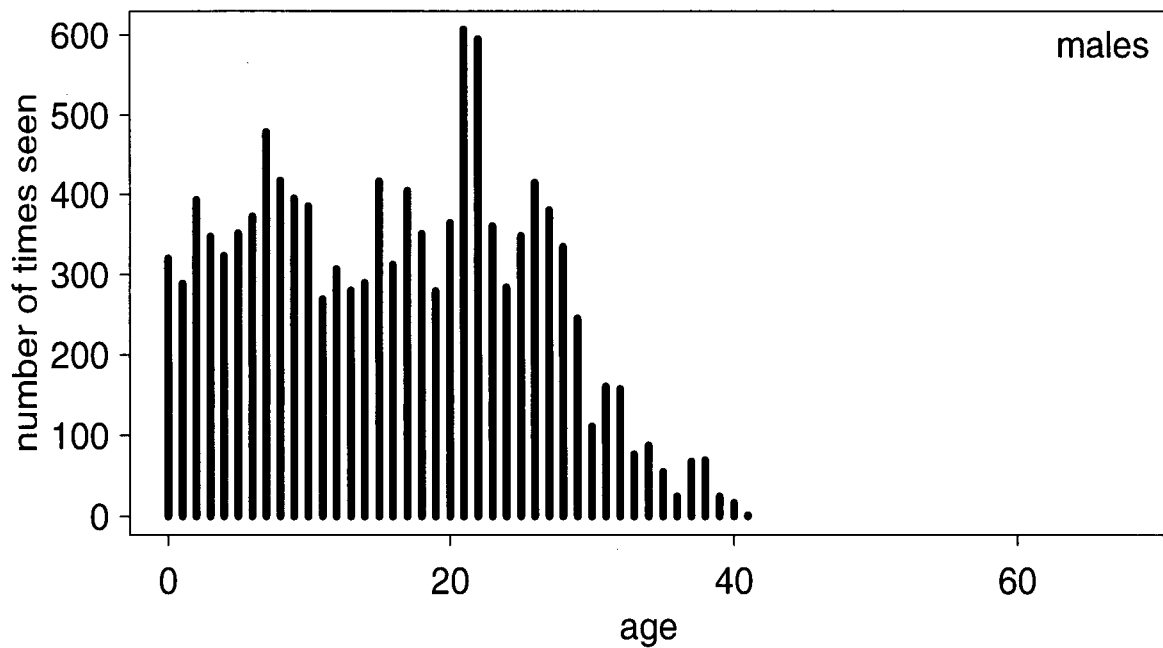
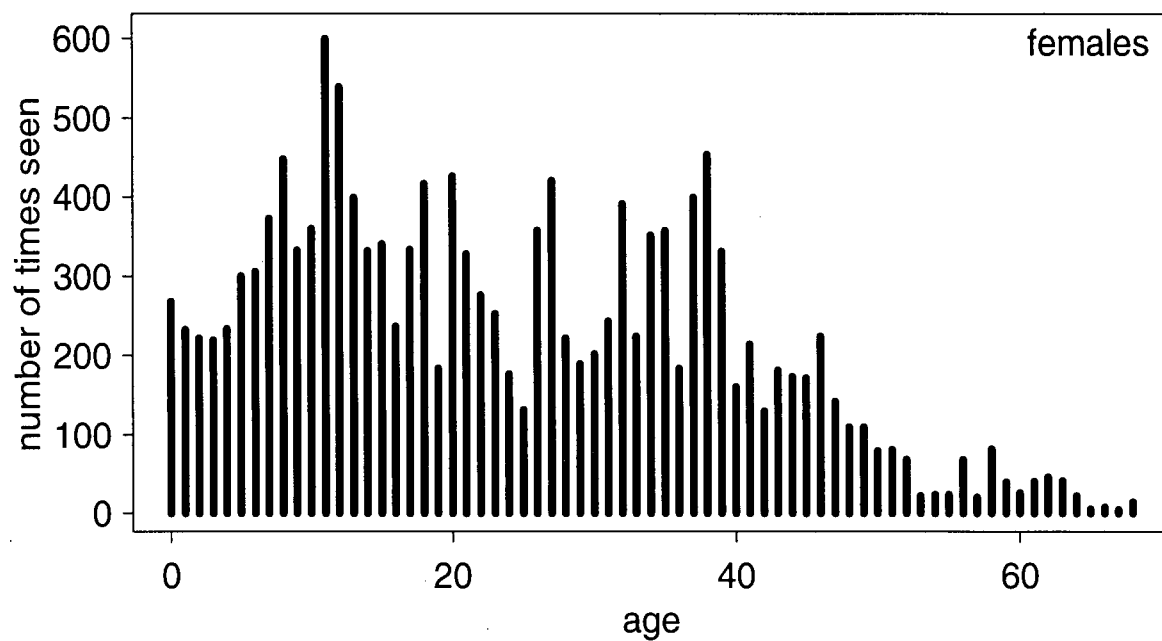


Last, I checked for sex- and age-biases in the photographic records. Figure 4 shows the number of times seen (frames) for whales of each age. Males seem slightly more often photographed than females, but there is no obvious pattern by age that is not demographic (e. g. there are fewer older whales to be photographed than younger). Note the shorter life span of males. Females outlive males by at least 10 - 20 years (Olesiuk et al. 1990; and see Figure 4, page 8).

Making an association dataset

I discarded all records of single whales (i. e. whales seen alone) because those records do not contain information on social connections. This left me with records with two or more whales seen in the same frame, and a unique combination of information in all other fields. Further, I omitted columns that were of little or no use for my analysis, e. g. encounter number, visual entry, and comments. At this point the dataset was converted into a list of pairwise associations within each year. The number of times a given pair of whales was seen together, in the same frame, each year was counted, as was the number of frames in which each whale was photographed with at least one other whale. The algorithm was: for each whale in a given photo frame, (1) increment the number of times that whale was seen in association that year, and (2) increment the number of times it was seen with each other whale within a frame that year. Note that a given frame generates pairwise associations with each of the whales as a focal animal. This is so the importance of different associates can be measured from each whale's perspective.

Figure 4. Distribution of photos taken by age in each of the two sexes, in the Bigg database.



To measure the importance of an associate to a given whale I used a simple ratio:

$$\frac{(\text{number of times whale A was seen with whale B in a given season})}{(\text{number of times whale A was seen with at least one other whale in that season})}.$$

I call this association index the "simple index". Note that because I dealt only with ID-transcripts of the original photographs, I could not determine any spatial relationships among the whales in a frame.

Adding demography

For identifying and grouping the associations between individuals, two kinds of categories were added: sex-dependent age classes, and relationship types based on known matrilineal genealogy.

Whales were assigned to ten sex/age classes. The female classes were: calves, immatures, subadult, reproductive females, and post-reproductive females. Males were classed as: calves, immatures, juveniles, subadult, or adult (Table 1). Sex/age class boundaries were chosen *a priori* according to previous convention and what is known about killer whale biology. Estimated birthdates for whales born prior to 1973 were taken from Bigg et al. (1990). The most recent births, from 1973 to 1992 were documented and provided by Ellis and Ford (Ford et al. 1994). Individuals of unknown sex (n=66) were excluded from the analysis.

The sex/age classes were chosen on the basis of the following assumed criteria: *female calves* are dependent neonates; *immature females* are young whales still dependent on their mother's care for survival; *subadult females* are non-dependent whales which are going through either physical or behavioural change before they reach adulthood;

Table 1. Age classes of female and male killer whales

age/sex	classes	age ranges in years	term used
Females			
F1		0 - 2	calf
F2		3 - 7	immature
F3		8 - 13	subadult
F4		14 - 39	reproductive
F5		> 39	post-reproductive
Males			
M1		0 - 2	calf
M2		3 - 10	immature
M3		11 - 14	juvenile
M4		15 - 20	subadult
M5		> 20	adult

reproductive females are mothers; and *post-reproductive females* are those which haven't had a calf for at least 10 years. *Male calf* and *immature* categories were the same as for females; *juvenile males* are young males that exhibit the onset of the secondary dorsal fin growth; *subadult males* are still in the growth phase; and *adult males* are those whose dorsal fin growth had stopped (as determined through photographic comparison by Bigg et al. 1990). Because the sexes exhibit differences in development and biology, the age range in each class is different for each sex. The age ranges according to the above criteria are those used in the definitions of Table 1.

All associations involving individuals of known sex and age were assigned to relationship types on the basis of known genealogy (Table 2). The maternal genealogy was determined through photoidentification, association and direct observation by Bigg et al. (1990). I assumed Bigg et al.'s genealogy to be true since Bain (1989) verified the genealogy and suggested only minor alterations. The degree of relatedness between whales born prior to 1973 was an estimate based on Cole's association index and direct observation by Bigg and coworkers (Bigg et al. 1990). Paternity is unknown, therefore no father, grandfather, or paternal uncle or aunt relationship types were assigned. Relationship types were grouped according to the degree of relatedness as: 1) immediate kin; 2) extended kin; or 3) non-kin (see Table 2).

Table 2. Relationship types and their codes (as used in Figure 15) categorized by kinship group.

immediate kin		extended kin		non-kin	
	code		code		code
mother-daughter	md	niece-aunt	nia	female-female	ff
daughter-mother	dm	niece-uncle	niu	female-male	fm
mother-son	ms	nephew-aunt	nea	male-female	mf
son-mother	sm	nephew-uncle	neu	male-male	mm
sister-sister	ss	aunt-niece	ani		
sister-brother	sb	aunt-nephew	ane		
brother-sister	bs	uncle-niece	uni		
brother-brother	bb	uncle-nephew	une		
		female-female cousin	fkif		
		female-male cousin	fkim		
		male-female cousin	mkif		
		male-male cousin	mkim		
		gran*-granddaughter	gd		
		gran*-grandson	gs		
		granddaughter-gran*	dg		
		grandson-gran*	sg		

gran*=grandmother

My Association Dataset

Through the steps described above, I constructed a derivative of the Bigg dataset to serve as the master dataset for all my subsequent analysis. I call this my Association Dataset and its properties, contrasted with the Bigg dataset, are summarized in Table 3. Table 4 shows a 10-record excerpt of the association dataset as an example of its structure and content.

Patterns in Associations

I started the investigation of patterns of associations by counting the number of observations of each relationship type. Table 5 shows these counts categorized by relationship type and kin group. I noticed that associations involving males were more frequent than those involving females. To show this clearly, I paired homologous relationship types that differ in the sex of the focal animal (Table 6).

In almost all cases the relationship pairs with males as the focal individual were observed more often. These results are rather surprising because the sex ratio is about even. In fact, the number of whales involved in this study showed a slight bias in the opposite direction (95:81 in favour of females). The results suggest that males are more social (i. e. seen more often in association) than females. Next, I repeated the procedure as above, but with the median age of the whales observed in each type of association. In Table 7, the results are listed in homologous pairs of relationship types, differing in the sex of the focal animal. In each pair (focal median with homologous focal median, non-focal with non-focal) the larger median age is written in bold.

Table 3. Comparison of the " Bigg" and "Association" datasets.

Property	Bigg dataset	Association dataset
communities	northern and southern residents & transients	northern residents
time of year	all months	only July-September
records selected	all	no consecutive identicals, only records with > 1 whale in frame. No unknown sexes
number of records	> 43802	9879
number of whales	237	176
fields	date	focal whale ID
	encounter number	associate ID
	photographer	year
	location	total times seen in association
	film roll number	times seen with associate
	frame number	association index
	visual entry	sex of focal
	whale IDs	age of focal
	comments	age class of focal
		sex of associate
		age of associate
		age class of associate
		relationship type

Table 4. Ten lines from the Association Dataset:

ID of focal	ID of associate	year	total n of focal	total n of whale pair	association index	sex of focal	age of focal	age class of focal	sex of associate	age of associate	age class of associate	relationship type
A20	A32	83	11	6	0.545	M	30	M5	M	19	M4	une
A20	A32	84	3	1	0.333	M	31	M5	M	20	M4	une
A20	A33	73	13	1	0.076	M	20	M4	M	2	M1	mm
A20	A33	79	31	4	0.129	M	26	M5	M	8	M2	mm
A20	A33	84	3	1	0.333	M	31	M5	M	13	M3	mm
A20	A34	75	5	1	0.200	M	22	M5	F	0	F1	mf
A20	A34	76	16	1	0.062	M	23	M5	F	1	F1	mf
A20	A34	79	31	1	0.032	M	26	M5	F	4	F2	mf
A20	A36	73	13	1	0.076	M	20	M4	F	26	F4	bs
A20	A36	76	16	4	0.250	M	23	M5	F	29	F4	bs

Table 5. Number of observations in each relationship type categorized by kinship group.

immediate kin group		extended kin group		non-kin group	
	N		N		N
daughter-mother	367	aunt-niece	10	female-female	667
mother-daughter	367	niece-aunt	10	female-male	678
son-mother	427	uncle-niece	24	male-female	678
mother-son	427	niece-uncle	24	male-male	208
sister-sister	106	aunt-nephew	36		
sister-brother	302	nephew-aunt	36		
brother-sister	302	uncle-nephew	106		
brother-brother	258	nephew-uncle	106		
		gran*-granddaughter	25		
		granddaughter-gran*	25		
		gran*-grandson	54		
		grandson-gran*	54		
		female-female cousin	4		
		female-male cousin	90		
		male-female cousin	90		
		male-male cousin	61		

*gran = grandmother

Table 6. Comparison of number of observations of homologous relationship types. The paired types differ in the sex of the focal animal. The larger of the pair of numbers is in bold.

relationship type with male as focal	number of observations		relationship type with female as focal
<i>son</i> -mother	427	367	<i>daughter</i> -mother
<i>brother</i> -brother	258	302	<i>sister</i> -brother
<i>brother</i> -sister	302	212	<i>sister</i> -sister
<i>nephew</i> -aunt	36	10	<i>niece</i> -aunt
<i>nephew</i> -uncle	106	24	<i>niece</i> -uncle
<i>uncle</i> -niece	24	10	<i>aunt</i> -niece
<i>uncle</i> -nephew	106	36	<i>aunt</i> -nephew
<i>male</i> -female cousin	90	2	<i>female</i> -female cousin
<i>male</i> -male cousin	61	90	<i>female</i> -male cousin
<i>grandson</i> -gran*	54	25	<i>granddaughter</i> -gran*
<i>male</i> -male non-kin	208	678	<i>female</i> -male non-kin
<i>male</i> -female non-kin	678	667	<i>female</i> -female non-kin
total	2350	2317	

*gran=grandmother

Table 7. Comparison of median ages of associates. The relationship types are listed as homologous pairs which differ in the sex of the focal animal. Note that the larger median age of the focal animal in each pair is written in bold.

relationship type with male as focal			median age	relationship type with female as focal		
<i>son</i> -mother	12	37	11	35	<i>daughter</i> -mother	
<i>brother</i> -brother	17	17	12	16	<i>sister</i> -brother	
<i>brother</i> -sister	16	12	12	12	<i>sister</i> -sister	
<i>nephew</i> -aunt	4	12	5.5	17	<i>niece</i> -aunt	
<i>nephew</i> -uncle	8	24	5	22.5	<i>niece</i> -uncle	
<i>uncle</i> -niece	22.5	5	17	5.5	<i>aunt</i> -niece	
<i>uncle</i> -nephew	24	8	12	4	<i>aunt</i> -nephew	
<i>male</i> -female cousin	27.5	22	5.5	5.5	<i>female</i> -female cousin	
<i>male</i> -male cousin	23	23	22	27.5	<i>female</i> -male cousin	
<i>grandson</i> -gran*	5	48	2	45	<i>granddaughter</i> -gran*	
<i>male</i> -male non-kin	17	17	26	17	<i>female</i> -male non-kin	
<i>male</i> -female non-kin	17	26	21	21	<i>female</i> -female non-kin	

*gran = grandmother

The results in Table 7 show that in almost all homologous relationship pairs with a male focal, the male focals are photographed at an older age and with older associates. To elaborate, females are more often observed in association when they are younger, and also more often observed with younger associates. Males are more often observed in association at older ages and with older whales, than are females. This is another surprising result because females have greater longevity than males, living on average about 20 years longer (Olesiuk et al. 1990). The association patterns thus do not appear to be a mere consequence of demography.

To further examine the age structure of each relationship type, I created a plot that contained information about the age of both the focal and the non-focal animal. For each pair in each year (pair-year), I plotted the age of the non-focal animal versus the age of the focal animal. Since age is only an integer value, there is potential for two different associations to have the same "coordinates". To avoid point overlap, both the x and y values were "jittered" so that the number of visible points on the plots is the number of observed pair-years of that relationship type. These age-age plots show striking patterns, and the complete set is included in the Appendix. A demographic trend is expected in this kind of plot because when a whale is young most potential associates are older, and when it is old, most of the population is younger. The following plots illustrate patterns that oppose expectations based on demography.

Associations between daughters and mothers cease around age 20 years rather abruptly (Figure 5). A demographic break-up in the daughter-mother relationship type might be expected in later life when mothers die. However, juxtaposition of the son-

Figure 5. Observed pair-years of the daughter - mother relationship type. There is a noticeable dropout by the time the daughters reach age 20.

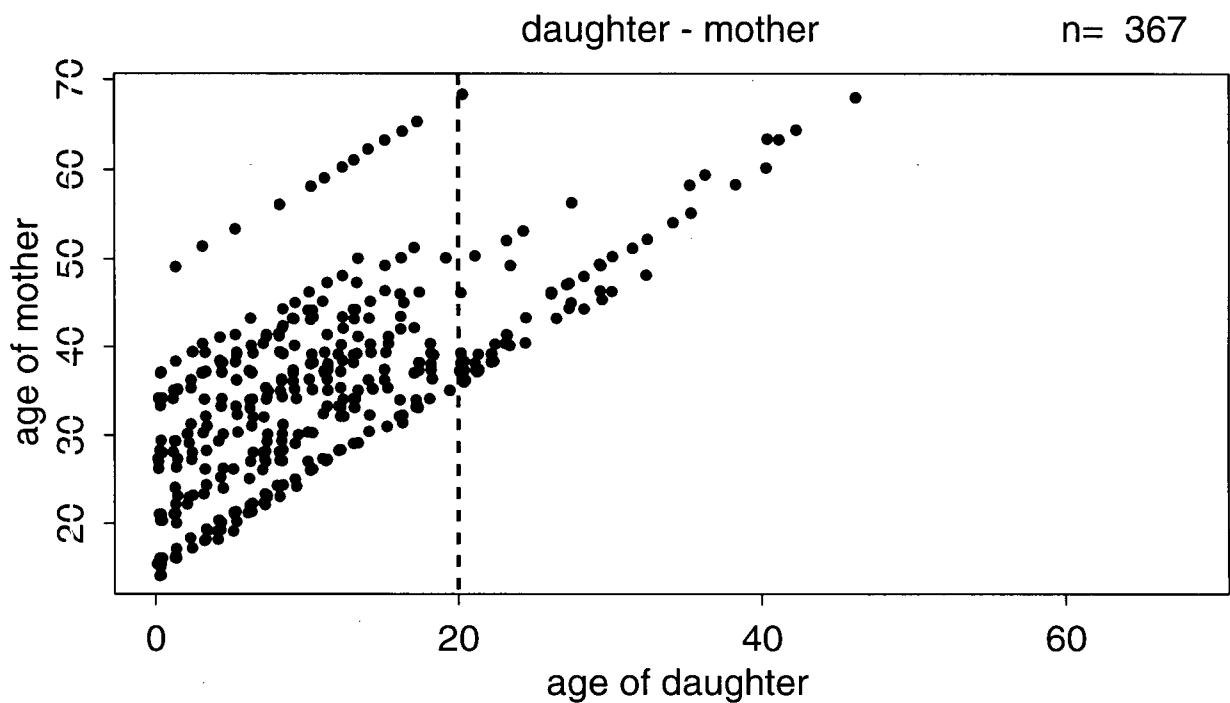
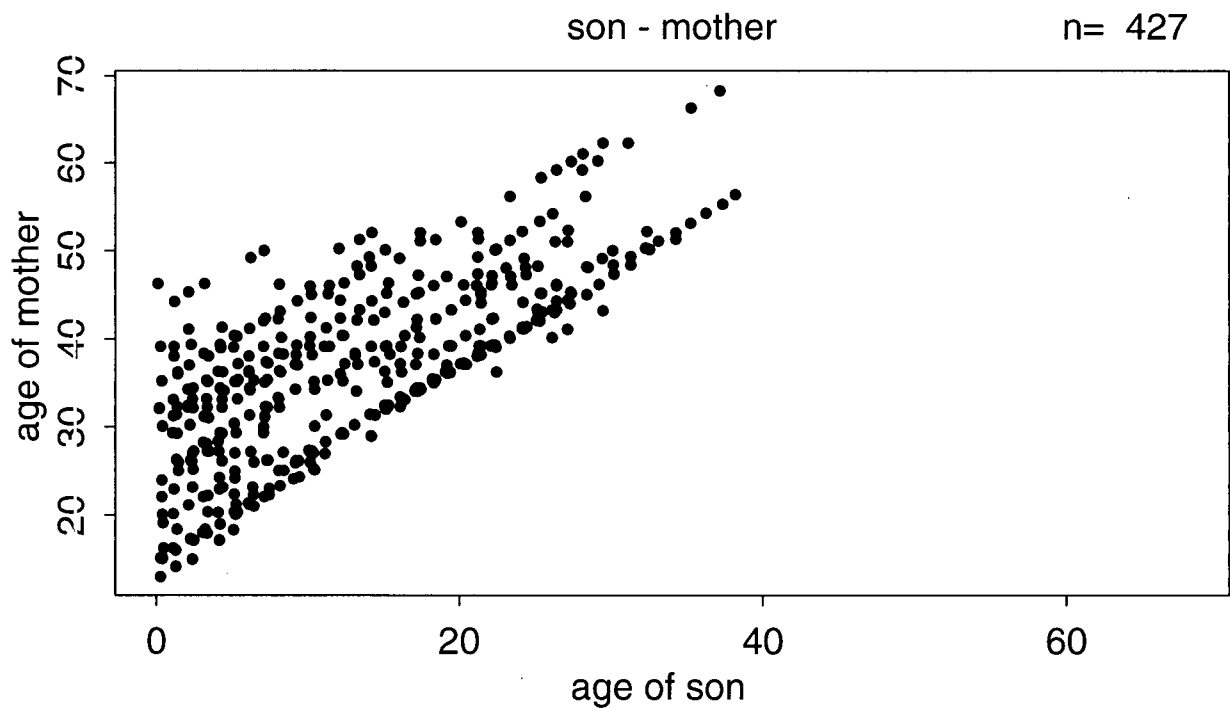


Figure 6. Observed pair-years of the son - mother relationship type. Pairs are continuously observed throughout the lifespan of the sons (typically 35-40 years).



mother plot (Figure 6) shows that mothers are usually still alive after their sons reach 20 years of age.

The sister-sister plot (Figure 7) shows a total lack of observed associations between sisters after age 29 years, although we know that females can live over 50 years (see Figure 4, & Olesiuk et al. 1990), and that sisters remain within the same pod. That the sisters are present and available for association is proven by the sister-brother plot (Figure 8), which records associations at ages older than 29 years.

The male-female cousin plot shows a data gap at the other end of the age spectrum (Figure 9). Although there were few associations between males and their female cousins until the males reached age 21, after that age there are many observed associations with female cousins of the same, older and younger age. So we know that these female cousins existed all along, but were simply not seen with their male cousins when those males were young. This plot (Figure 9), like the previous results, shows that associations among the members of a pod are definitely not random. The pattern in Figure 9 could have various causes. Two possibilities are: (1) adult males start to seek out their female cousins at age 21, and (2) at age 21, males suddenly become attractive to female cousins of all ages. To support either alternative one can note that wandering whales, or those actively seeking social interaction, are likely to be seen in association more often, and with a more diverse set of associates than non wandering whales. If males, aged 21 or older (adult males) are doing the wandering, then they should be seen more often with male cousins as well: data in Figure 10 show that they are. If females of all ages wander towards adult males, then females should be seen more often with adult brothers, adult nephews, and adult uncles. However, any such pattern could just as easily be the result of the wandering adult males.

Figure 7. Observed pair-years of the sister - sister relationship type. Note that sisters are never seen with each other after age 29.

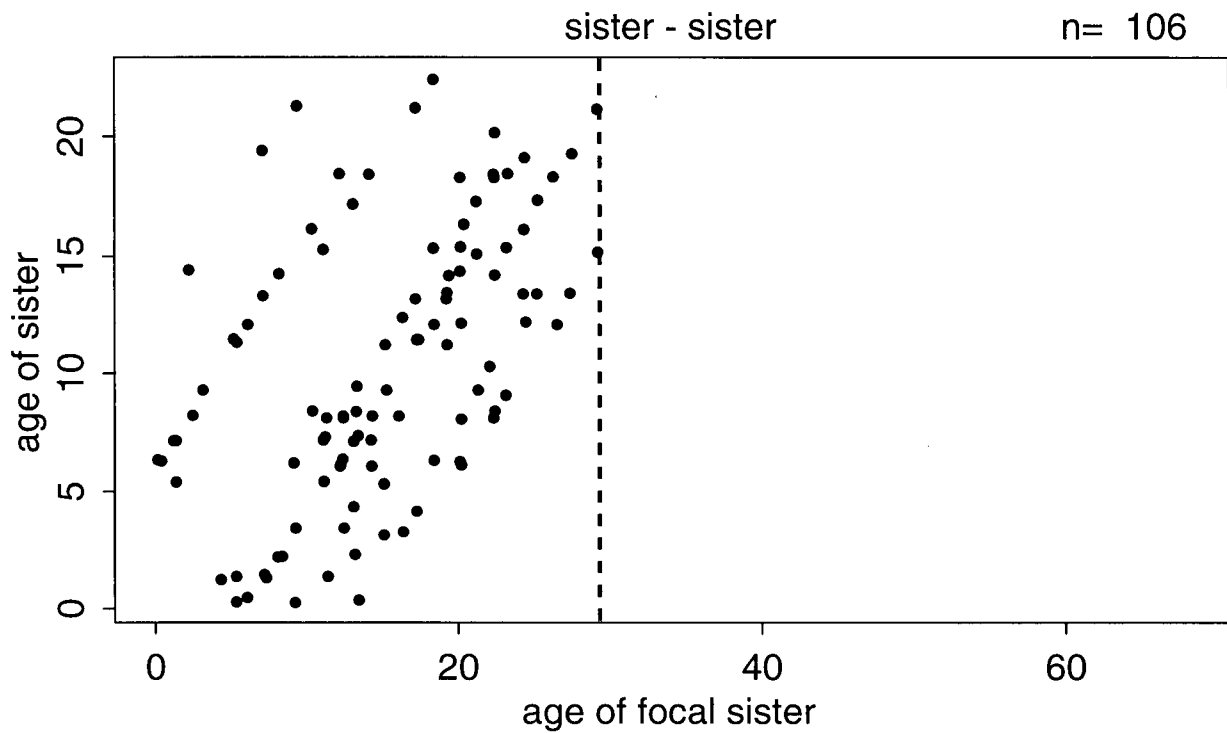


Figure 8. Observed pair-years of the sister - brother relationship type. Note that sisters are seen with their brothers throughout their brothers' lifespan (typically 35-40 years).



Figure 9. Observed pair-years of the male - female cousin relationship type.
Note the sudden increase when the males reach age 21.

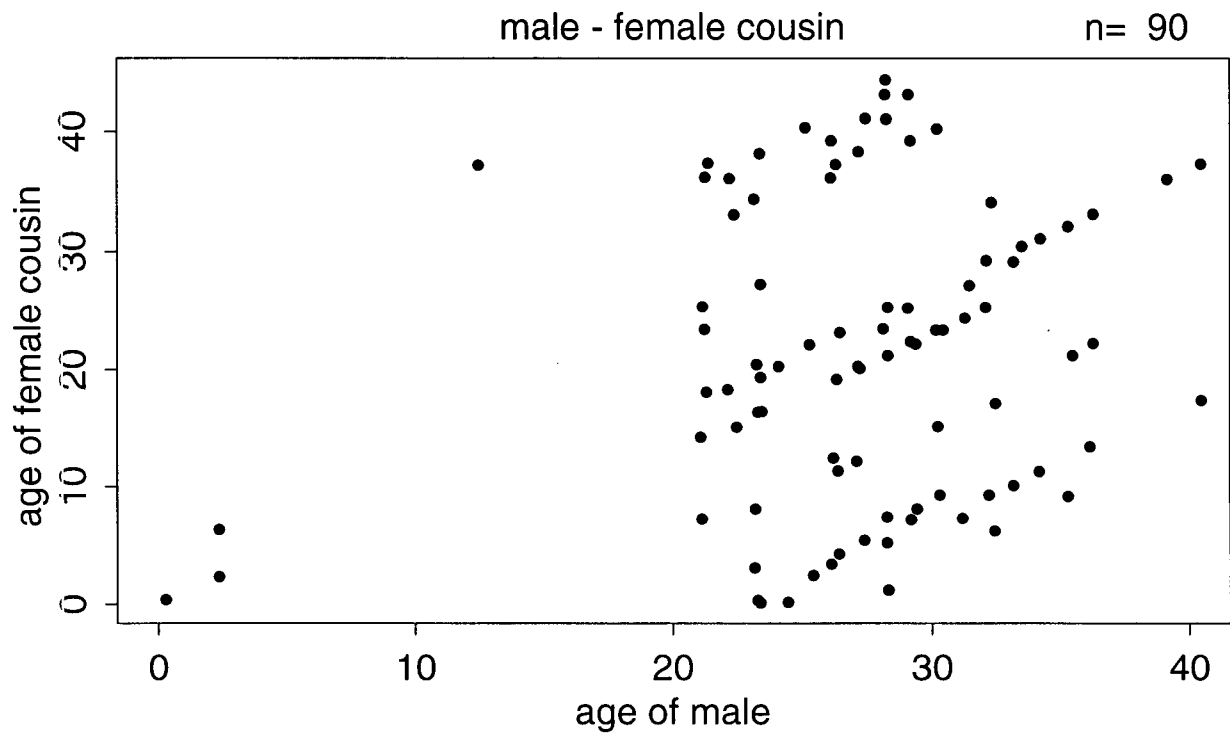
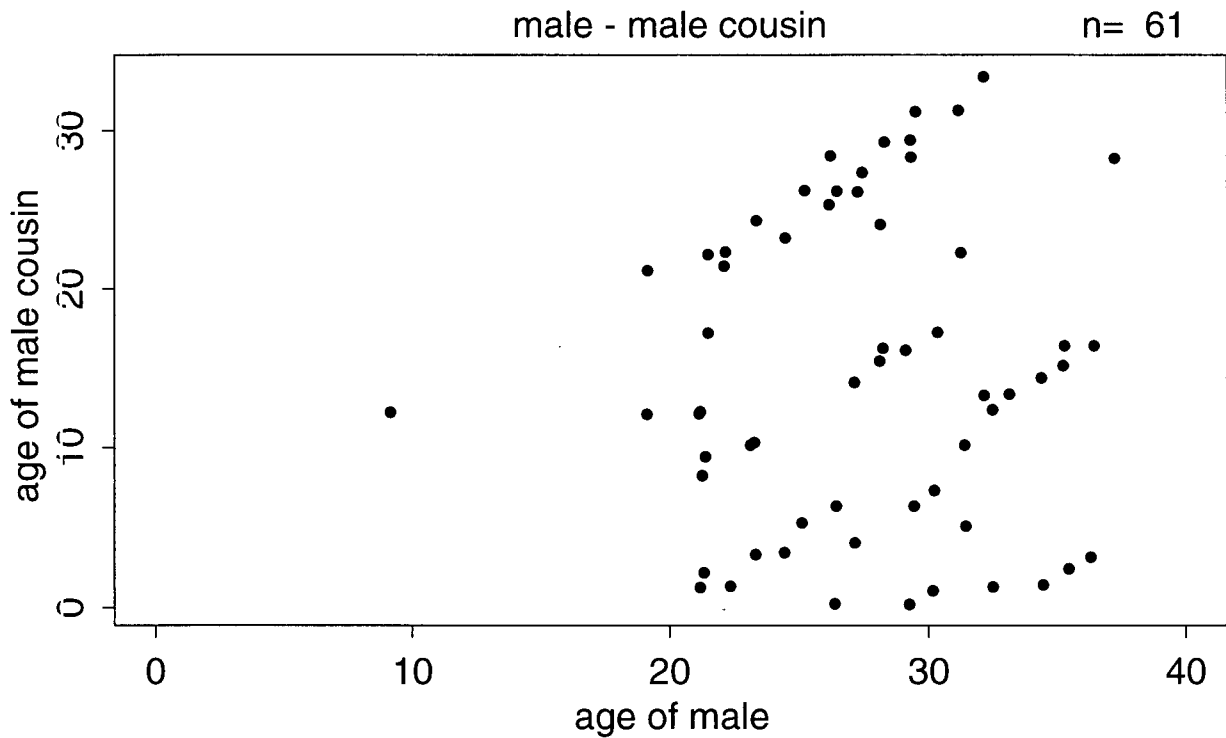


Figure 10. Observed pair-years of the male - male cousin relationship type.
Note that the associates of younger males are almost always older than 21.



One way to detect who is doing the wandering is to pick a group of whales of a given age range that is not wandering, and see who they are associating with. This 'fixed' group should be seen more often with the wandering sex-age categories. If we assume that young whales, say less than 10 years old, are likely to stay close to their mothers, then one can examine who comes by to "visit" them. Possible pairs are niece-aunt, niece-uncle, nephew-aunt, and nephew-uncle.

Young nieces and nephews are seen much more often with their uncles than with their aunts (Figures 11 through 14). Furthermore, young nieces are seen three times as often (counts = 21:7) with uncles aged 21 years or older than with younger uncles (Figure 12).

The evidence so far indicates that after males reach adulthood (age 21) they become more social. To further investigate this I examined the diversity of social contacts by age. I counted the number of associations of each relationship type and plotted them by age class (Figure 15). Note that these observations are not scaled according to the number of potential associates in each relationship type, so they do not indicate preference. They merely show relative numbers of social contacts. Furthermore, the barplots of each of the three kinship groups are scaled separately, so as not to lose detail. The relative numbers within each of the kinship groups can be compared across age-classes and sexes.

The females' main social focus appears to be their mothers when young (as calves, immatures, and subadult) and their own offspring once they are mothers themselves (Figure 15). During their life, they exhibit only marginal social contact with members of any extended kin types. This marginal contact with extended kin vanishes once they reach

Figure 11. Observed pair-years of the niece - aunt relationship type.

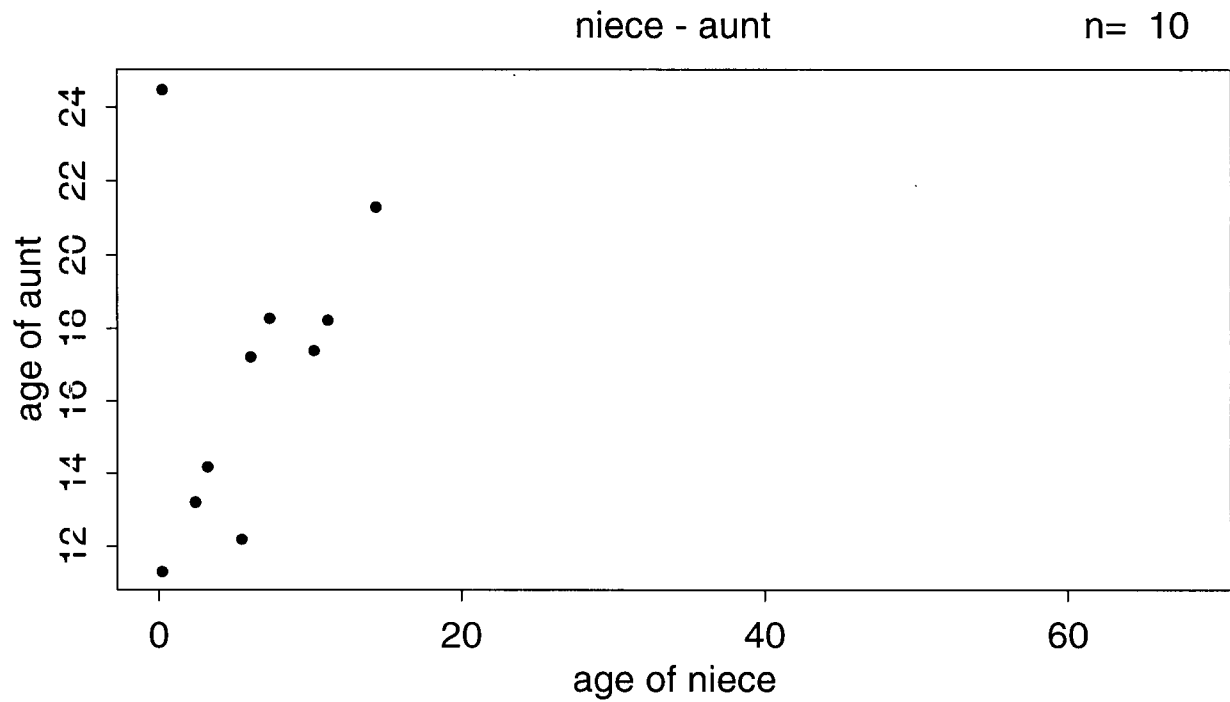


Figure 12. Observed pair-years of the niece - uncle relationship type.
Note that young females are more often seen with uncles than aunts (above).

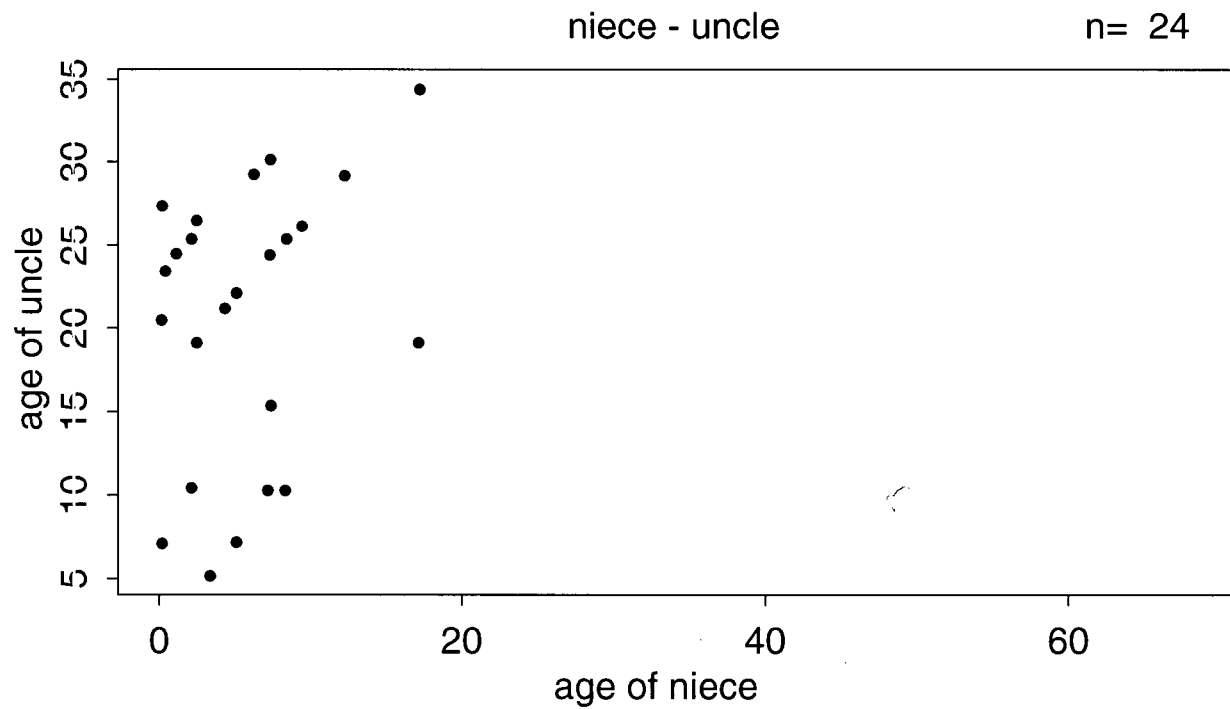


Figure 13. Observed pair-years of the nephew - aunt relationship type.

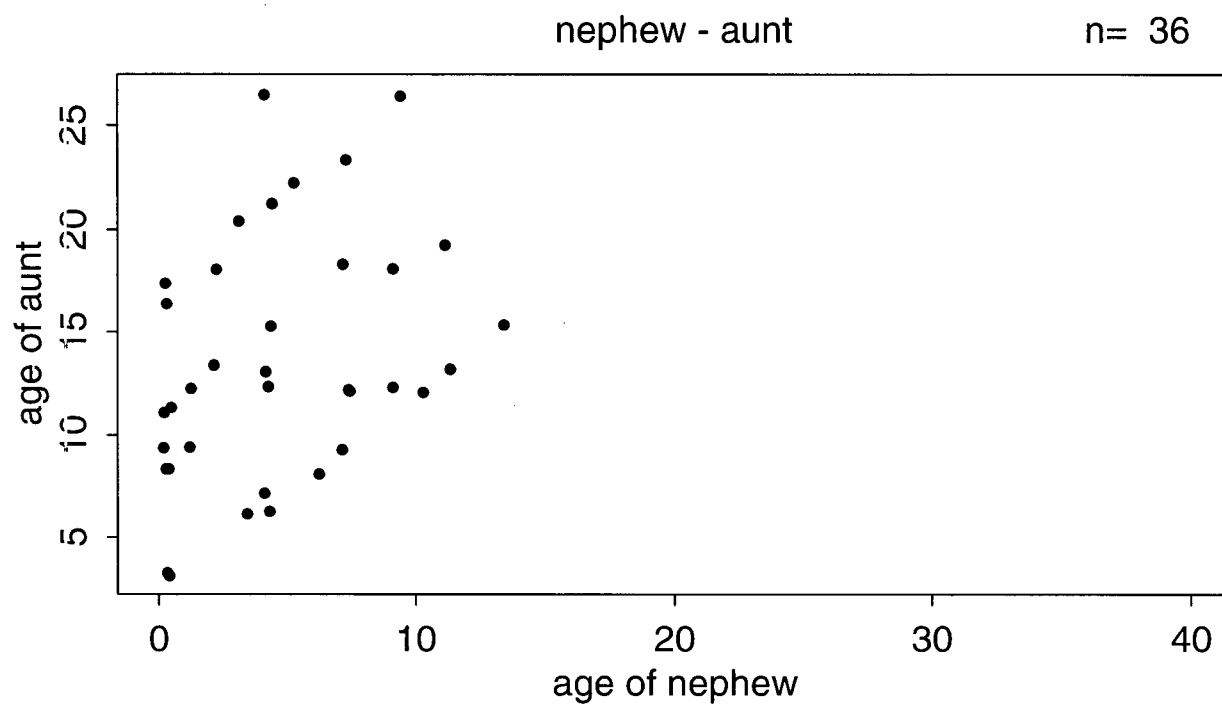


Figure 14. Observed pair-years of the nephew - uncle relationship type.
Note that young males are more often seen with uncles than aunts (above).

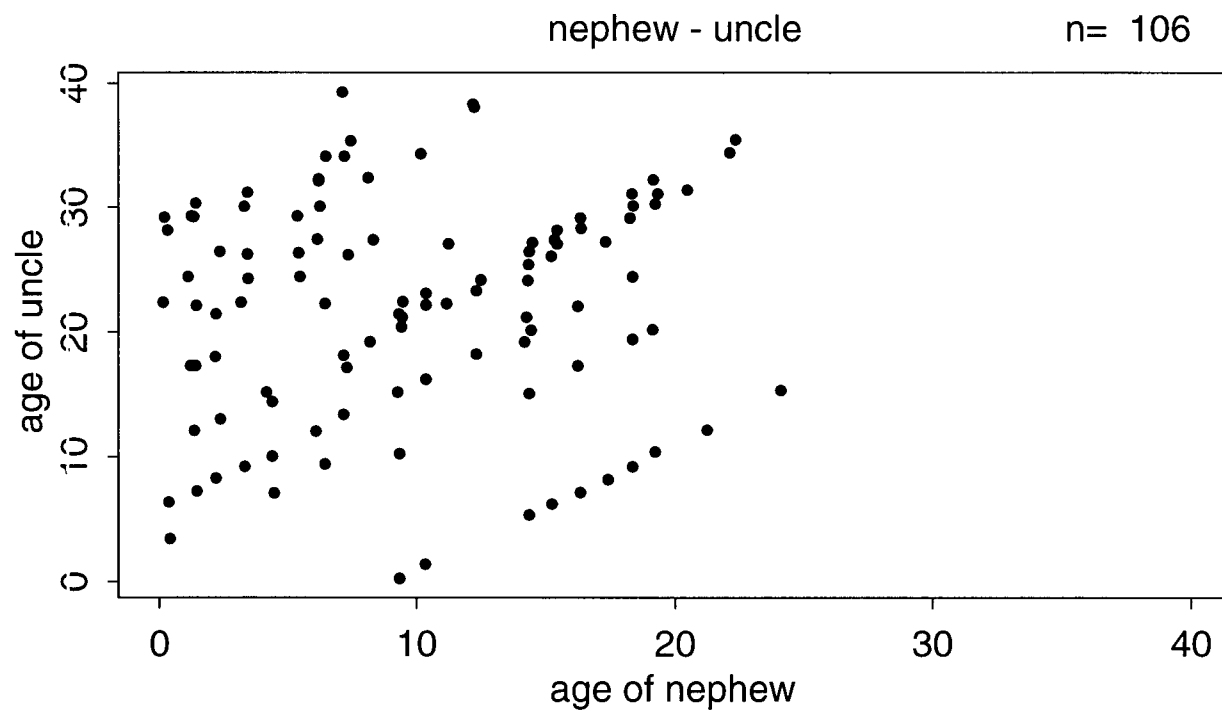
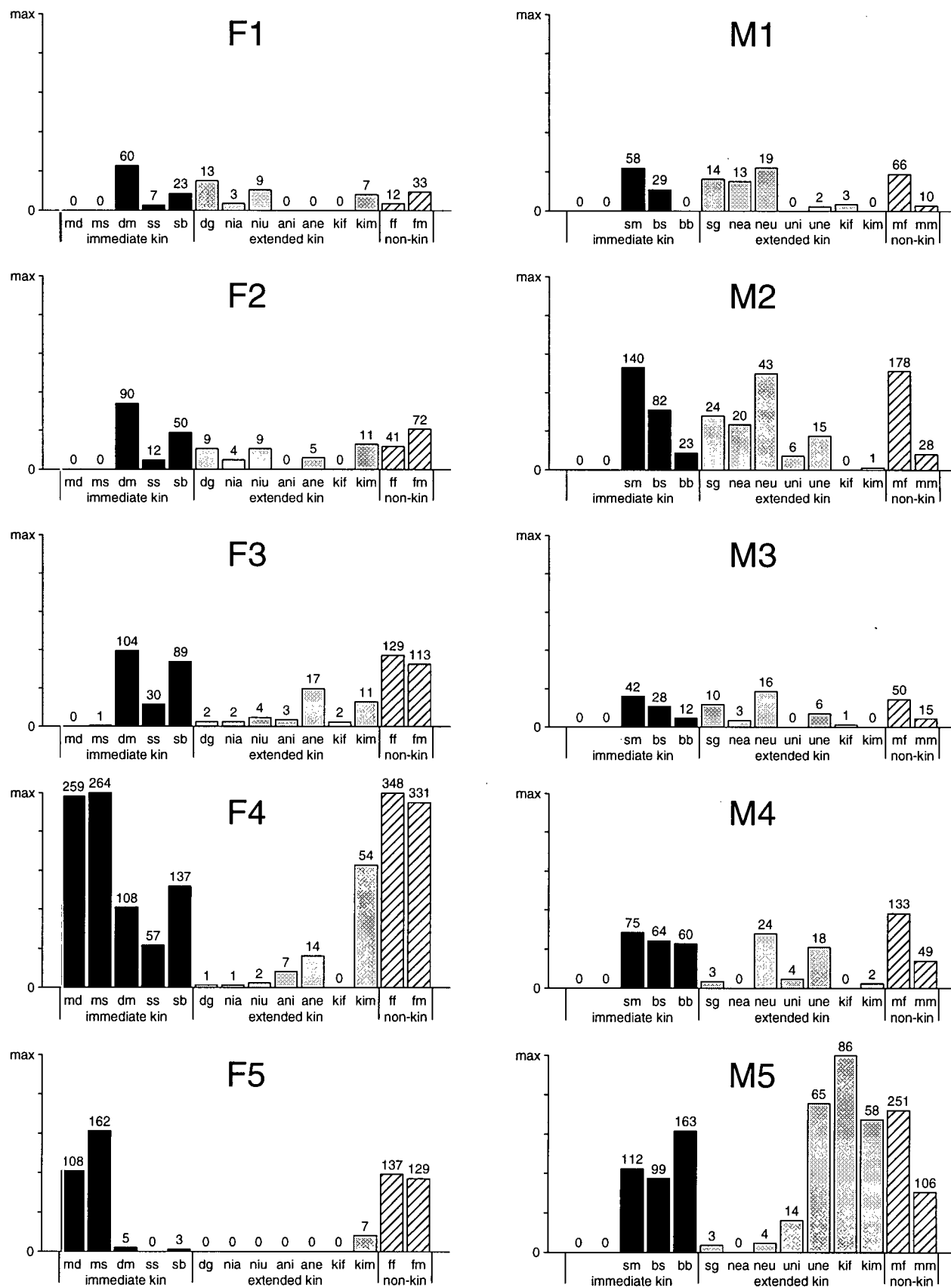


Figure 15. Observed associations by ageclass and relationship type. Kinship groups are scaled separately. See Table 1 for age ranges, Table 2 for relationship type codes.



the post-reproductive stage, at which point females are almost exclusively seen with their own offspring within a pod. Females of all age classes are seen more often with non-kin females than with non-kin males.

Male calves, immatures, and juveniles show high associations with their mothers as well as their siblings (Figure 15). Overall, males are seen more often with extended kin than are females. Once males reach subadulthood, they are seen with brothers most often. Members of the immediate kin group remain frequent associates of adult males, and there is an increase in associations with nephews, and female and male cousins as they grow older. This result supports the idea that once males reach adulthood they wander, and exhibit a greater diversity in their social contacts than do females within their pod. Non-kin males were photographed more often with non-kin females, but to a lesser extent than did females.

DISCUSSION

Bigg et al. (1990) defined sub-pods and pods by the (high) percentage of time that members were seen swimming together. The results of this study clearly show that although the whales in a pod do associate closely enough to be seen as a coherent group, the close association of pod members -- close enough and synchronous enough to be caught together in a single photograph -- is clearly non-random. Whales do not freely intermingle within the pod. This selectivity of association has been shown in other studies (Bain, 1988; Rose, 1992; S. Heimlich-Boran, 1988; Bigg et al., 1990), and the more or less independently swimming matrilineal units are recognized as sub-pods within a pod (Bain, 1988; Bigg et al., 1990). However, related females were not expected to be so isolated from each other within the same pod. The association patterns are strikingly different for males and females within pods.

Female Association Patterns

The results show that females are tightly bonded with only their mothers when young, and that once they become mothers themselves they associate almost exclusively with their own offspring. Young females (10 years old or younger) were seen less often than were young males with all possible relationship types except their mothers. Mothers show no sex bias in associations with their offspring. Females old enough to be mothers were photographed much less often than were males with all relationship types except non-kin females and males. No mothers were ever photographed with female cousins, and no sisters were photographed together after age 29 years.

Male Association Patterns

Males have more diverse social contacts than do females at all ages. Young males seem to be preferred over young females as associates by all whales except their reproductive-aged mother. When they reach adulthood (age 21), males show a sudden increase in social contacts, especially with their extended kin. There seems to be an affinity between the males of all ages within a pod.

Aunts and uncles are seen with young nephews much more often than with young nieces. The overall male affinity shows up, for example, in the greater numbers of uncle-nephew associations observed as compared with aunt-nephew pairs. Brothers are seen more often together than with their sisters, even at a young age. At older ages the brother-brother association becomes the most common one for males.

At age 21 there appears to be a striking change in the social life of male killer whales within a pod. This is most noticeable in the sudden appearance of numerous associations between adult males and extended kin females (cousins) of all ages. This increased social activity is apparent with other categories as well, such as with their male cousins and nephews. It would seem that this is the age at which males break free, to a certain extent, from the confines of their immediate family, their mother's matrilineal unit. However, males do continue to be seen with their mothers at a fairly constant rate for the rest of their lives, and the brother-brother association seems to increase in importance.

Pod Cohesion

Female social contacts with pod members are primarily *intra*-matrilineal unit contacts. *Inter*-matrilineal unit associations are dominated by males in all cases. Males are seen more frequently in association with pod members outside of their matrilineal unit, and no matter whether males were the focal and/or the non-focal of any homologous relationship type they were observed more often than females.

In contrast, females of all ages are seen more often with both male and female members of other pods (i. e. non-kin). In particular, across-pod associations are predominantly between females of reproductive age.

These patterns have ironic implications for pod cohesion, if one assumes that frequency of association is positively correlated with strength of social bond. It appears that female association patterns within matrilineally structured pods do very little to maintain pod cohesion. Female bonds are *intra*-matrilineal unit bonds, almost to the exclusion of the *inter*-matrilineal unit bonds that would bind together the various matrilineal units within a pod. Note for example the complete absence of sister-sister associations after age 29, in the 20 year long dataset. This lack of a female social network is unlike the social structure among other matrilineally organized species (Smuts 1988, 1987; Douglas-Hamilton 1975; Michener 1983, Fedigan 1982). In addition, the most frequent associations with members of other pods are between females. This pattern is unlikely to promote pod cohesion, and might even be an opposing force.

The association patterns of males are almost exactly complimentary to the female patterns. Males seem to provide the *inter*-matrilineal unit link within a pod, via

associations with extended kin of both sexes. This bonding is primarily due to *adult* males, with an emphasis on their bonds with males.

Other studies have noted that males are frequently seen with related males (Bain, 1989; Rose, 1992; S. Heimlich-Boran, 1988). Since these studies did not document the weak bonds of the females in a pod, they did not recognize the potential importance of male bonds in pod cohesion.

A Prediction

The results of this exploratory data analysis suggest that the main source of social cohesion within a pod is adult males. A smaller factor is the presence of non-adult males in other matrilineal units within the pod. The intra-matrilineal unit focus of females is a cohesive force only to the extent of the bonds between a mother and her daughters, who have their own matrilineal units, and sons.

Some predictions that follow from this analysis are:

1. a pod that lacks adult males will be low in cohesive social bonds.
2. a pod in which adult males exist, but in which some matrilineal units lack male members (young or not) will be less strongly bonded than a pod in which males are present in all component matrilineal units, and
3. a pod that loses a matriarch, a mother common to the mothers of the pod's component matrilineal units, will be less tightly held together.

A combination of these conditions can be expected to make pod-splitting more likely.

Known examples of pod-splitting

Eight matriarchs have died over the last twenty years, but only three pods have been observed to split. Four matriarchs (A01, A02, A14, A07) were survived by only one adult daughter and her own offspring and no split of the single remaining matrilineal units occurred. Two matriarchs (G12, A10) were survived by one adult son and two adult daughters each with their own offspring, and the two pods did not split. But one of these pods (A10) lost the adult male (brother) one year after the death of the common mother, and shortly thereafter the two remaining sisters began to split up. The seventh matriarch (J09) was survived by two daughters and their offspring, and the two sister matrilineal units seem to be gradually splitting (Bigg et al. 1990). When I reviewed the cases in which sisters split up, I found that only one of the two sisters had a male offspring, which was of juvenile age at the time of death of the adult uncle or the grandmother.

And the last matriarch (A09) left two adult sons and one adult daughter with her own matrilineal unit. Upon A09's death, the pod split along the brother-sister line. Pod A09 consisted of 7 members after the death of A09. Two adult brothers (A05, A26), their probable sister A08, her adult daughters (A28 and A42) and A42's two calves (A57+ A66) of unknown sex. I predicted on the basis of this study that the two calves of unknown sex would be females, or the adult males would have stayed with their sister's matrilineal unit. Shortly after I had made that prediction, A57 died and it was discovered to be a female (pers. comm. Barrett-Lennard). I expect time to show that A66 is also a female.

All of the observed pod splitting cases are consistent with the above predictions, which result from new perspectives on social structure gained in this study.

This study was undertaken to better understand the forces underlying *pod* cohesion, but we know that *communities* of pods also show a degree of cohesion. The northern residents do not mingle with the southern residents. Perhaps the bonds between non-kin females within the community are a source of “social glue” at the community level.

CONCLUSION

This study was done to understand the proximate causes of killer whale pod cohesion and pod splitting by studying social structure in the northern resident community in British Columbia. Investigation of female and male association patterns revealed that, despite the matrilineal organization of killer whale pods, kin females show a surprising lack of association with each other. The adult males of a pod play an important role in pod cohesion, linking two or more matrilineal units by associating with the male offspring of their sisters and aunts. Associations among non-kin females may link pods together as a community.

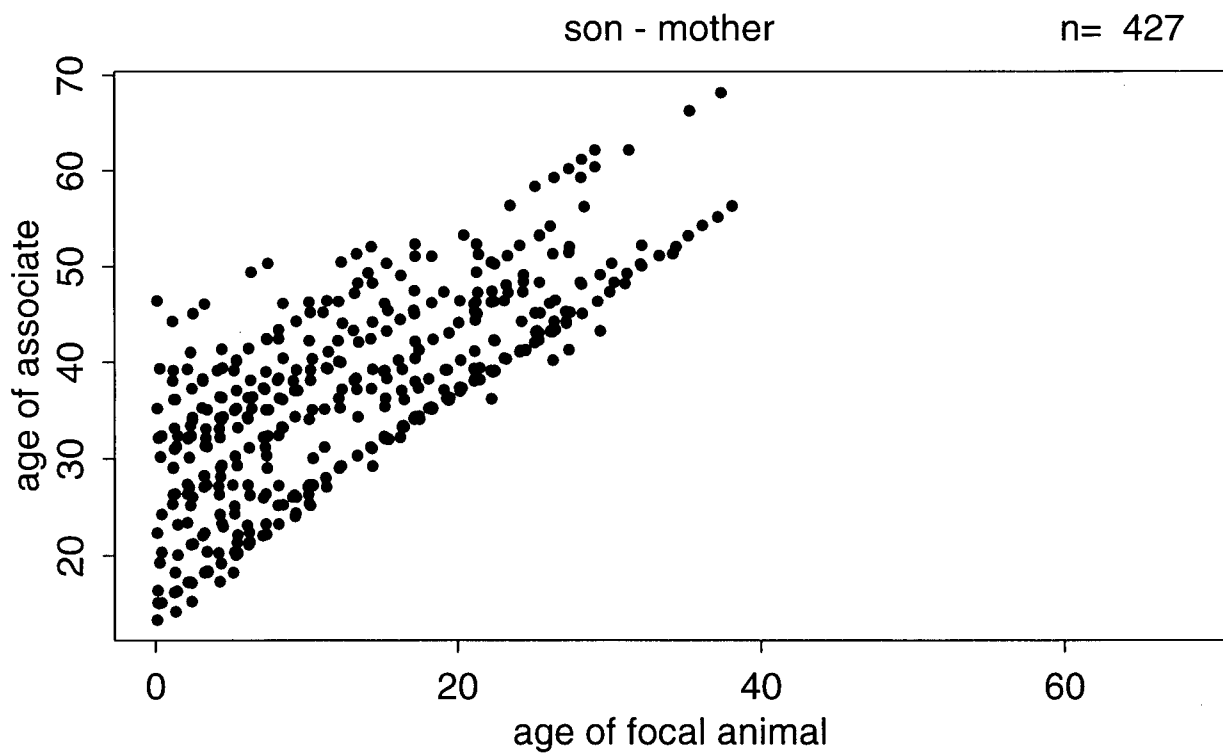
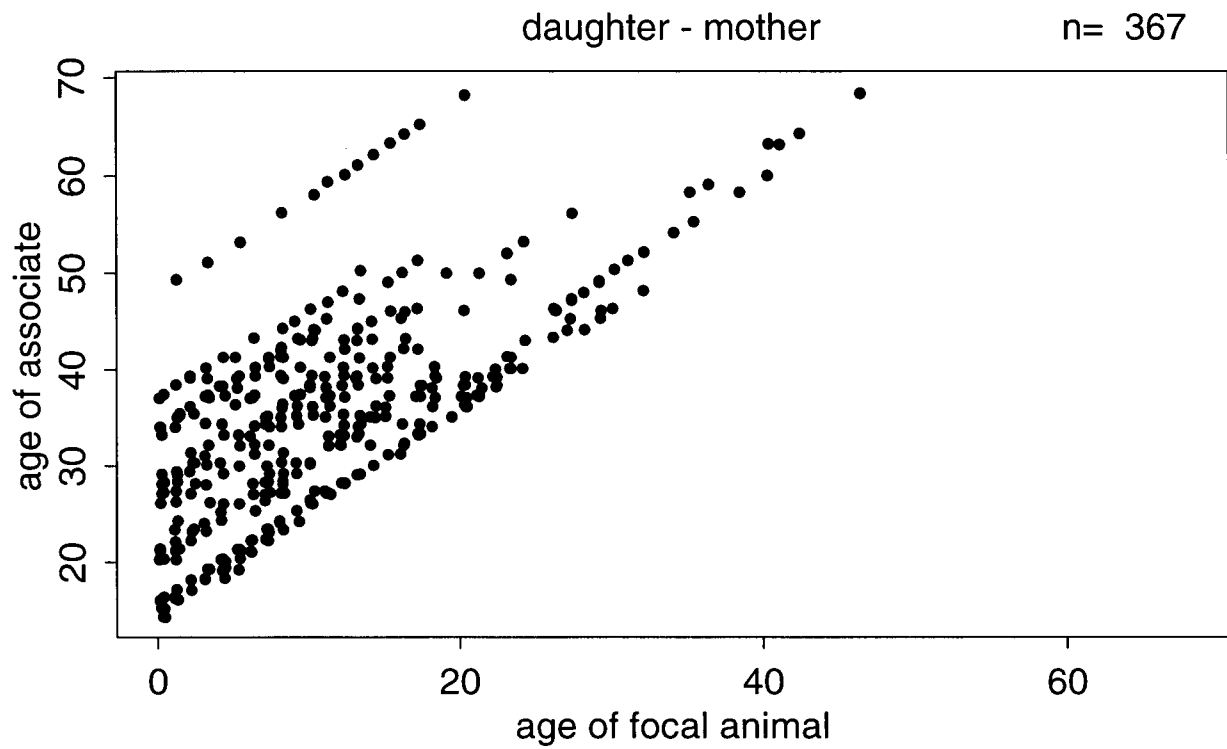
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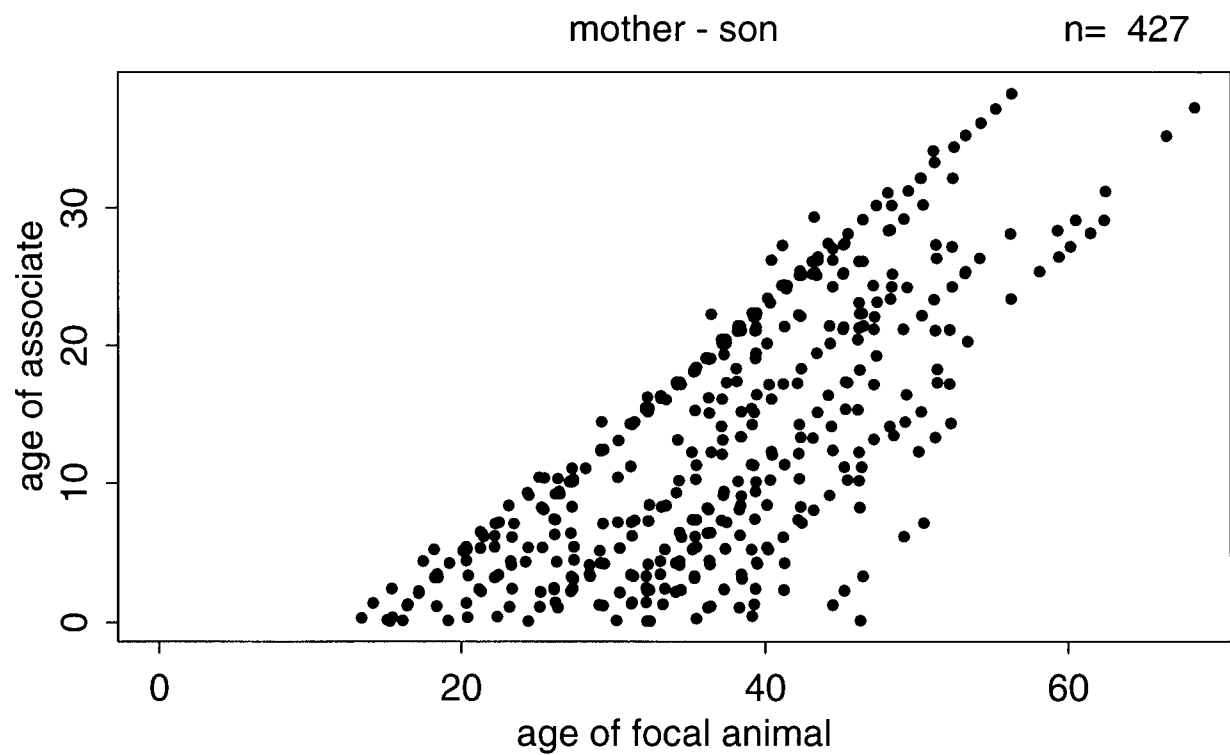
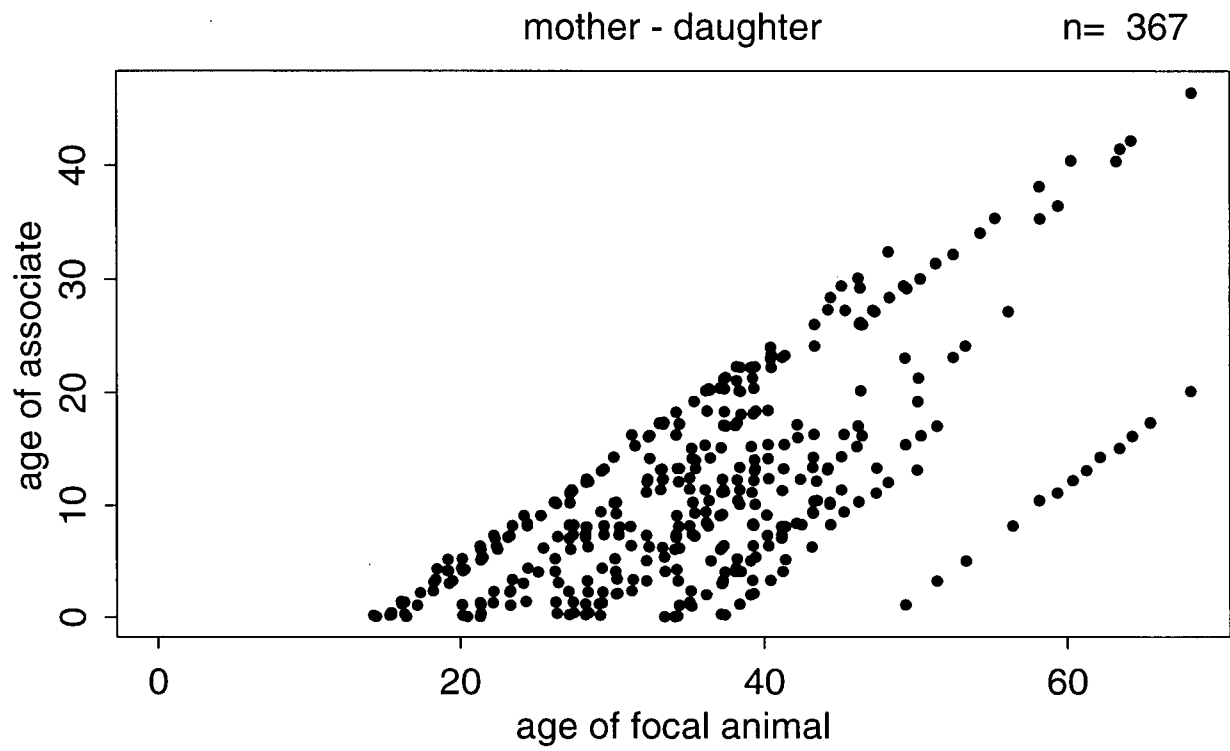
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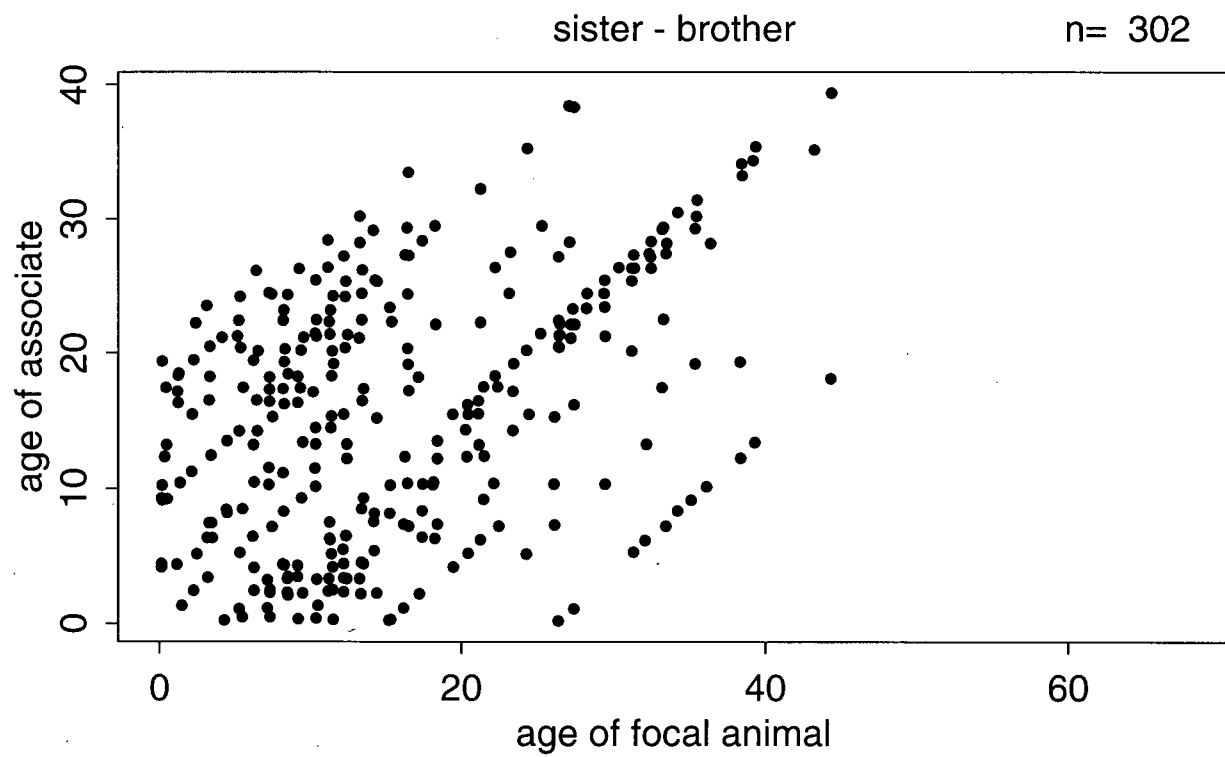
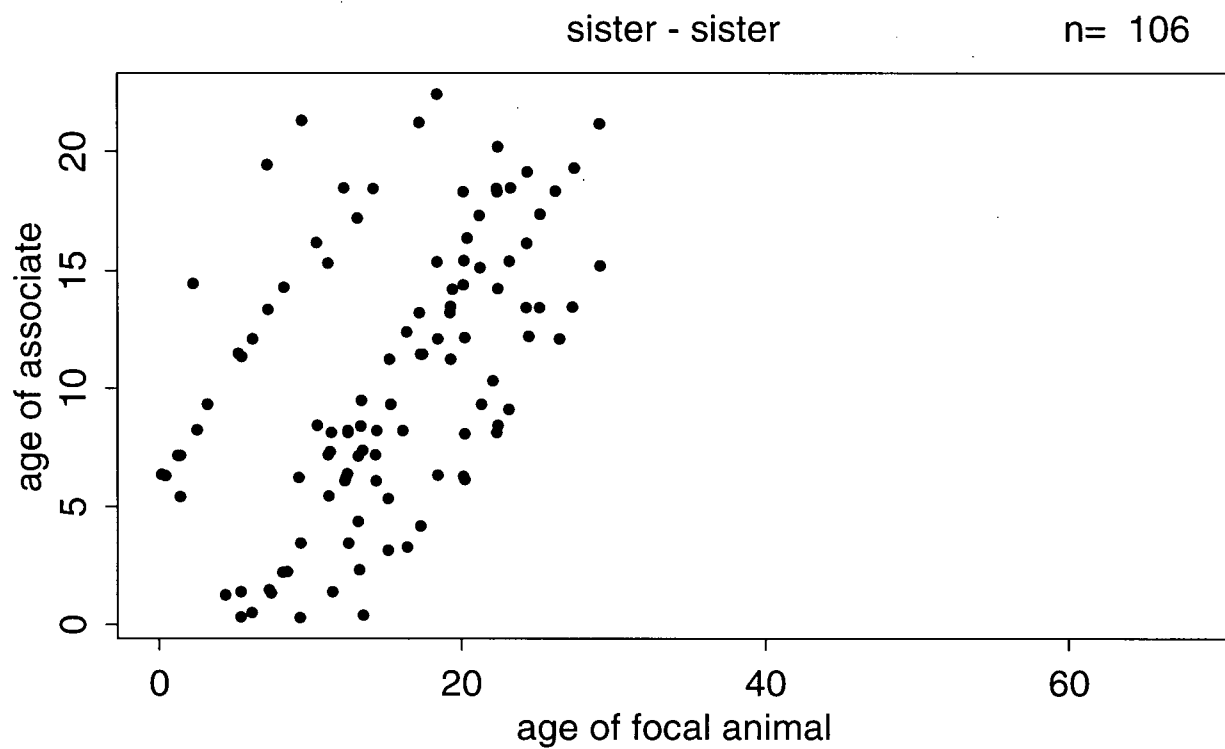
Appendix (pair-year plots)



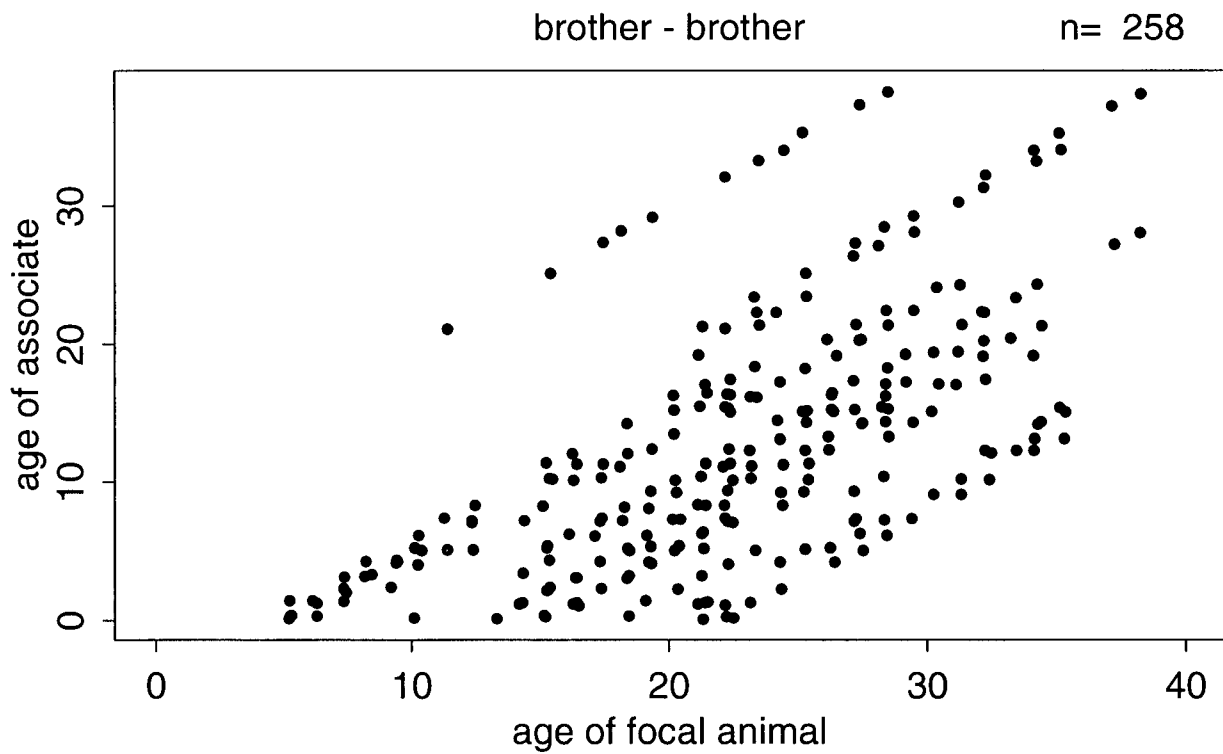
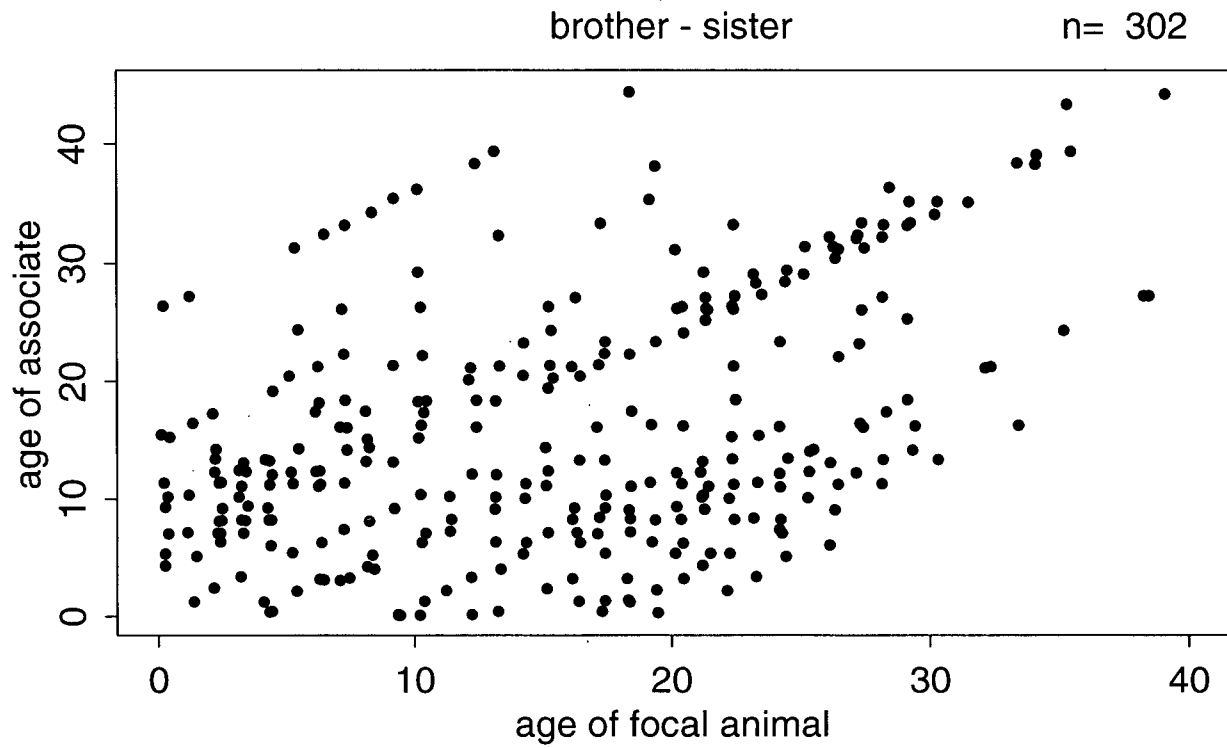
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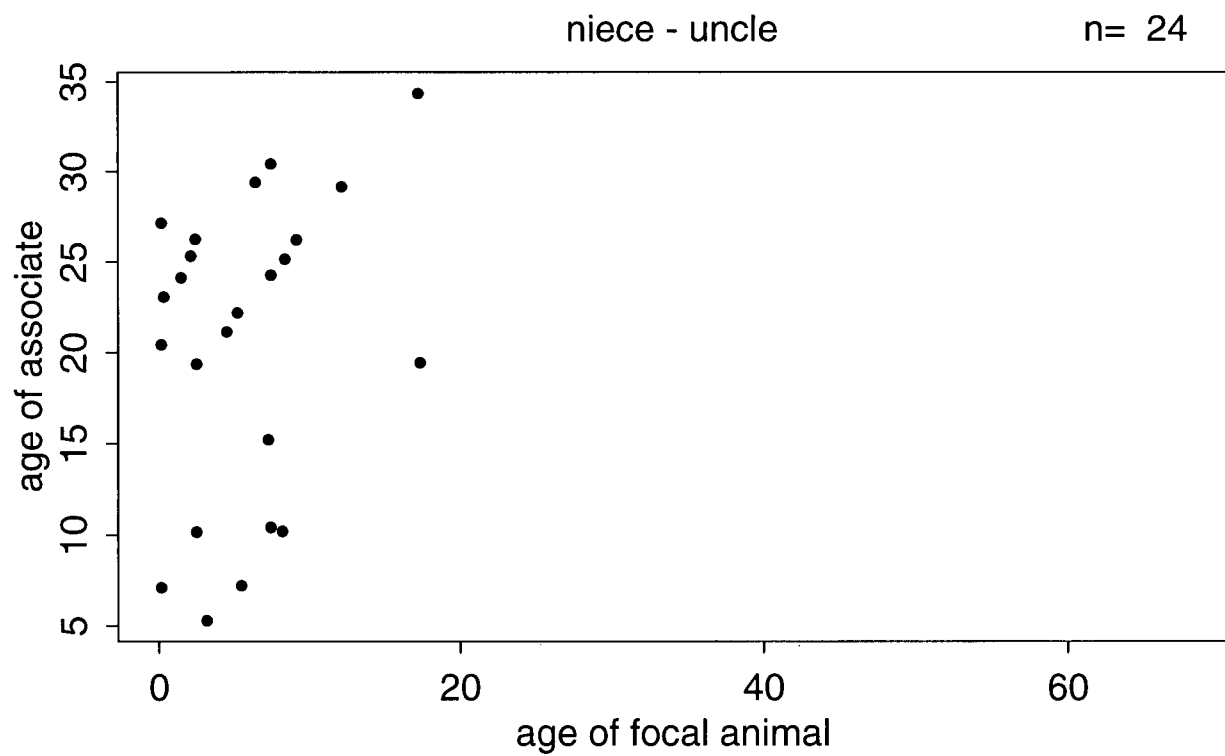
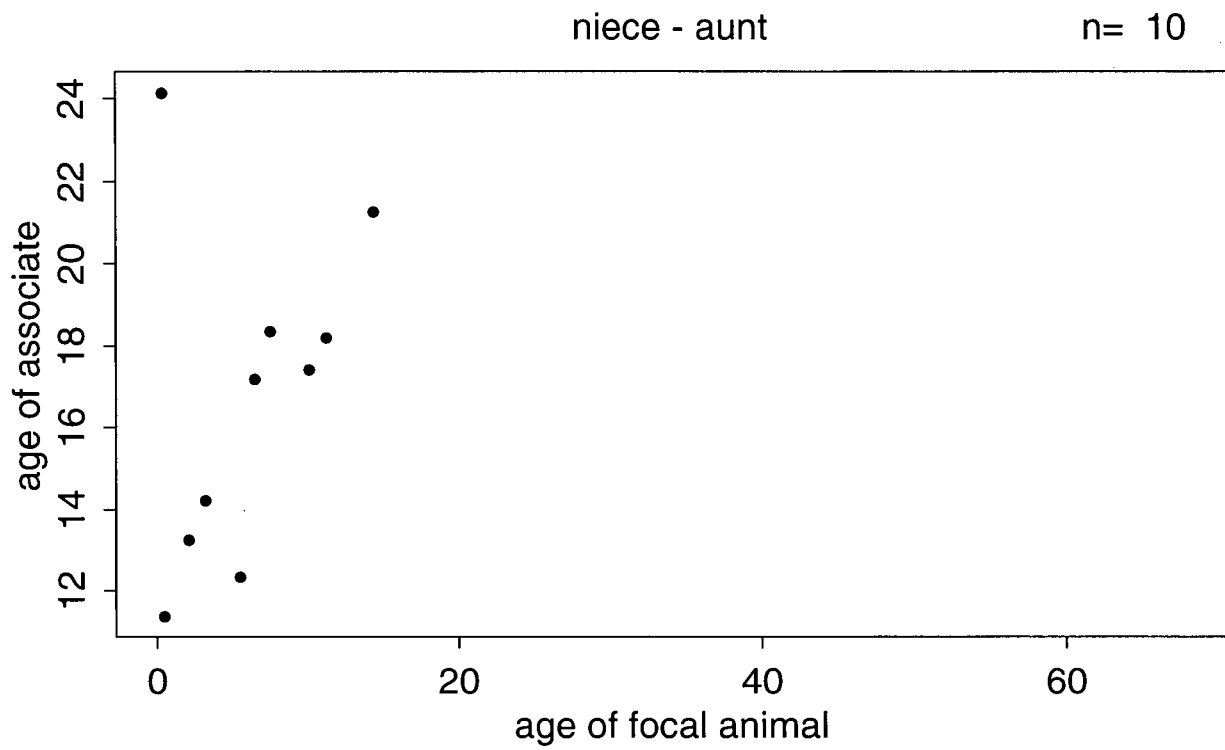
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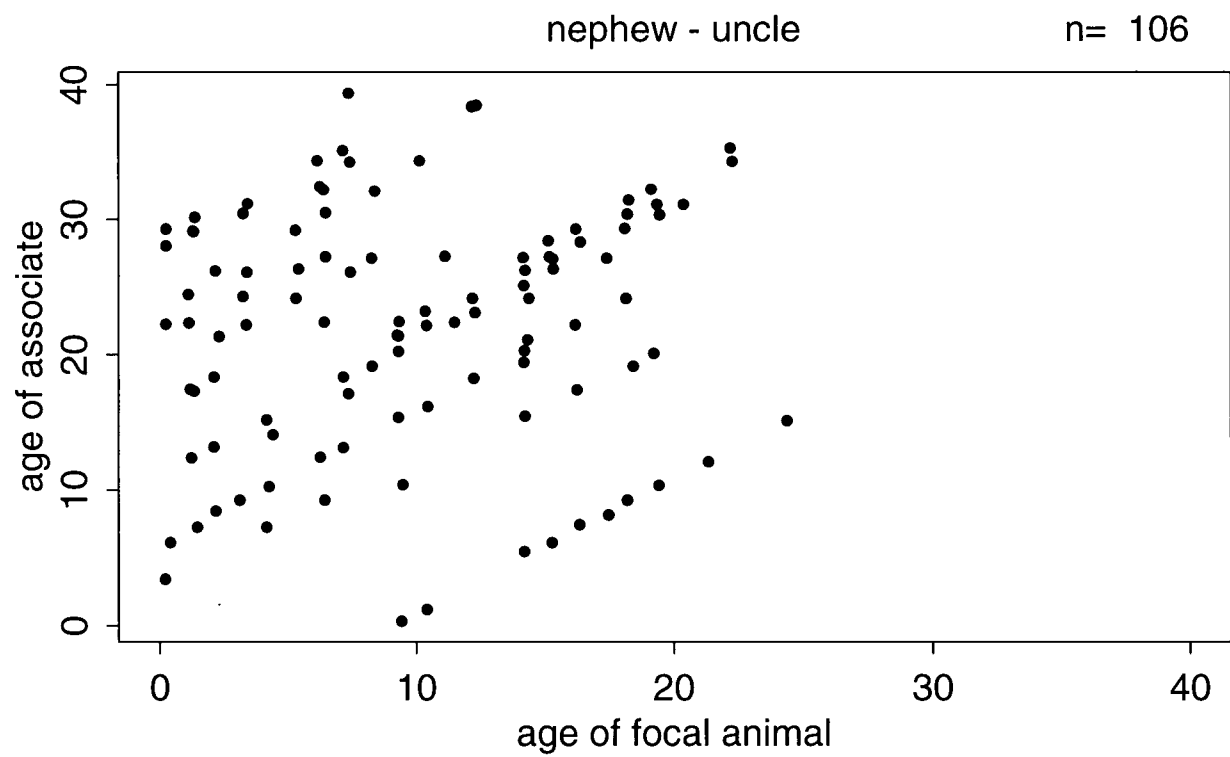
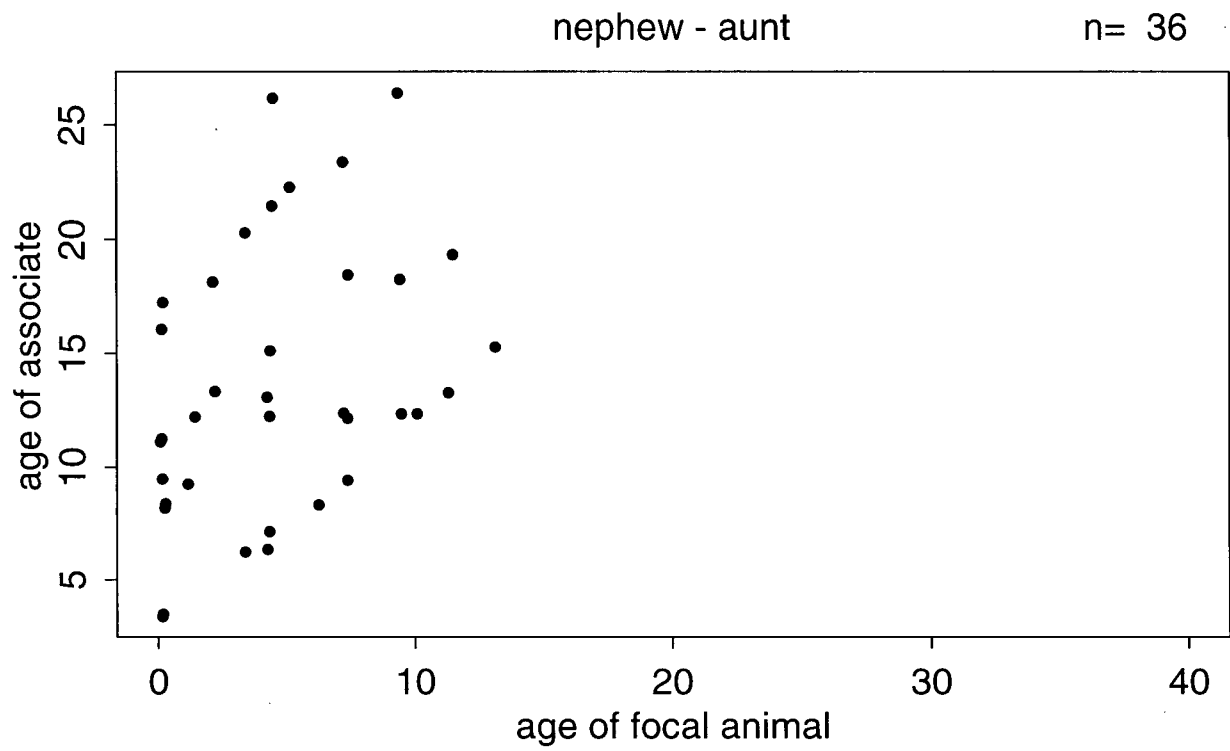
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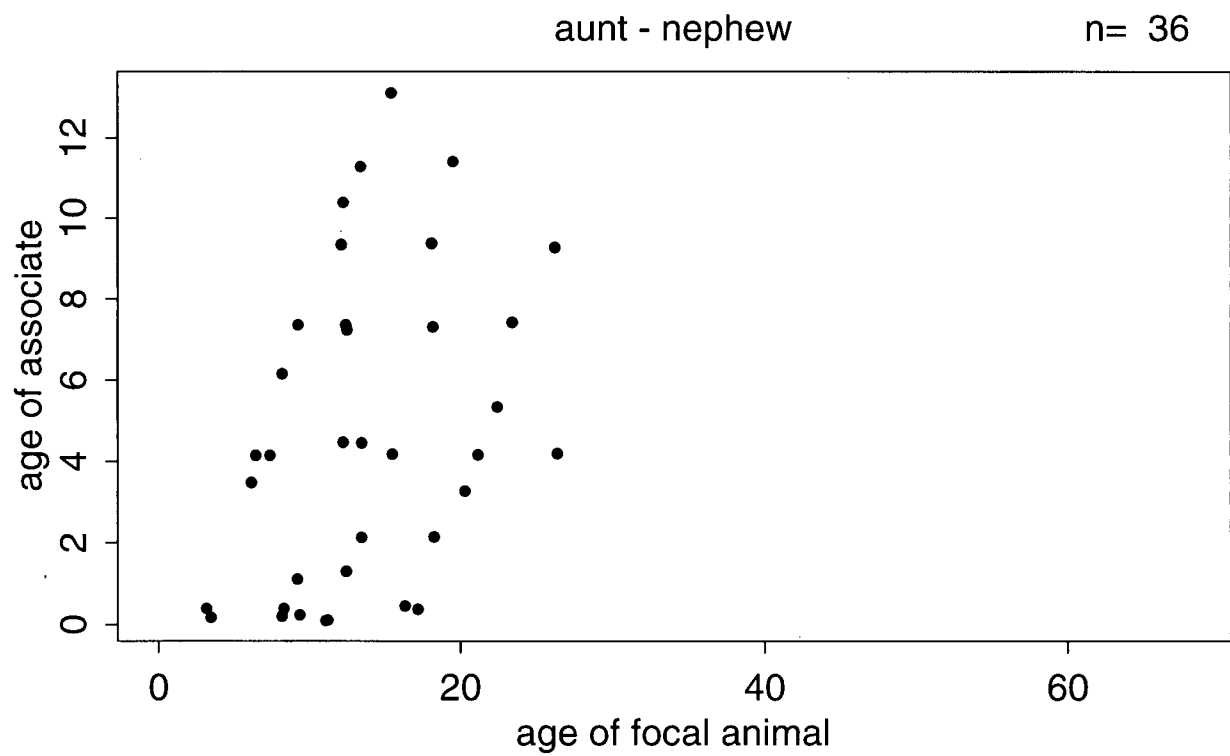
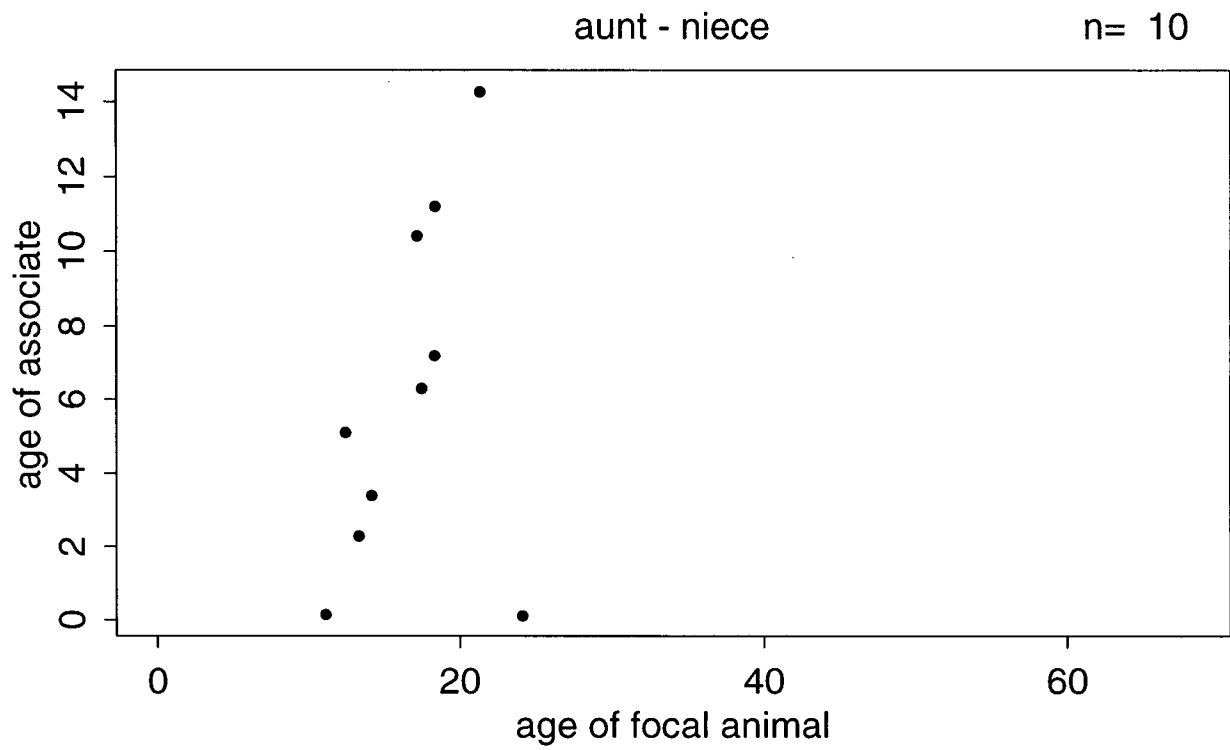
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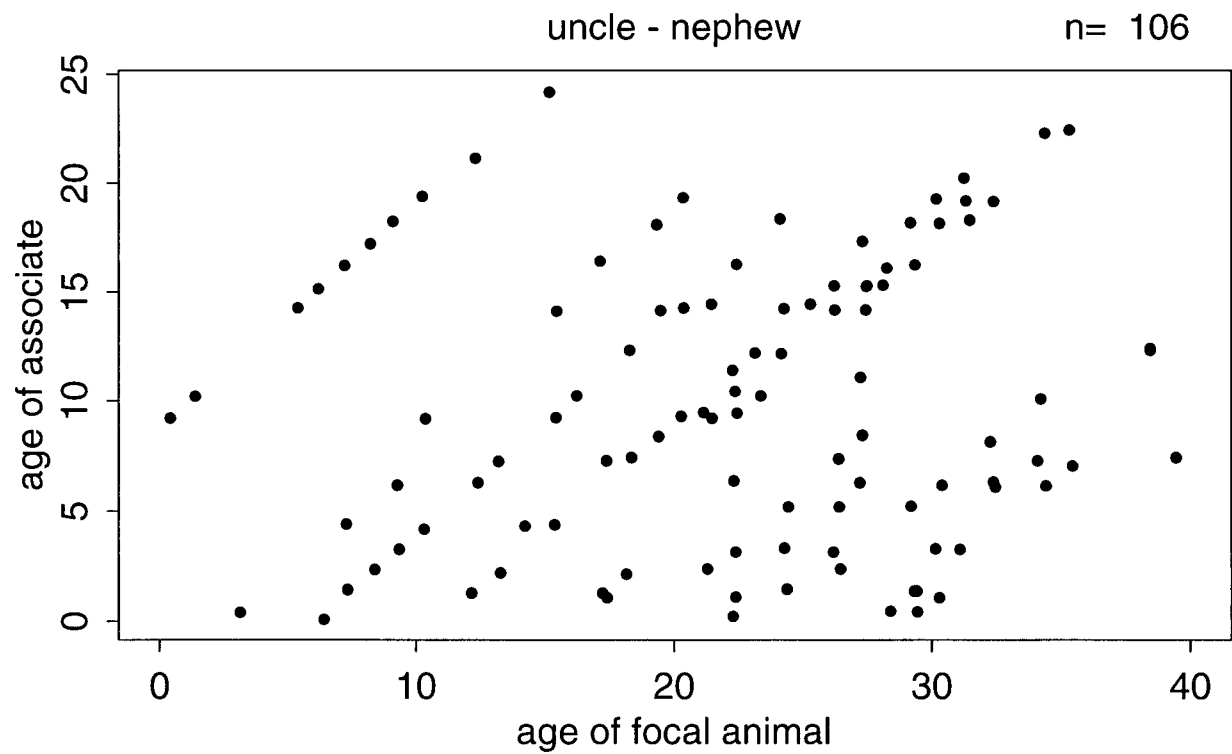
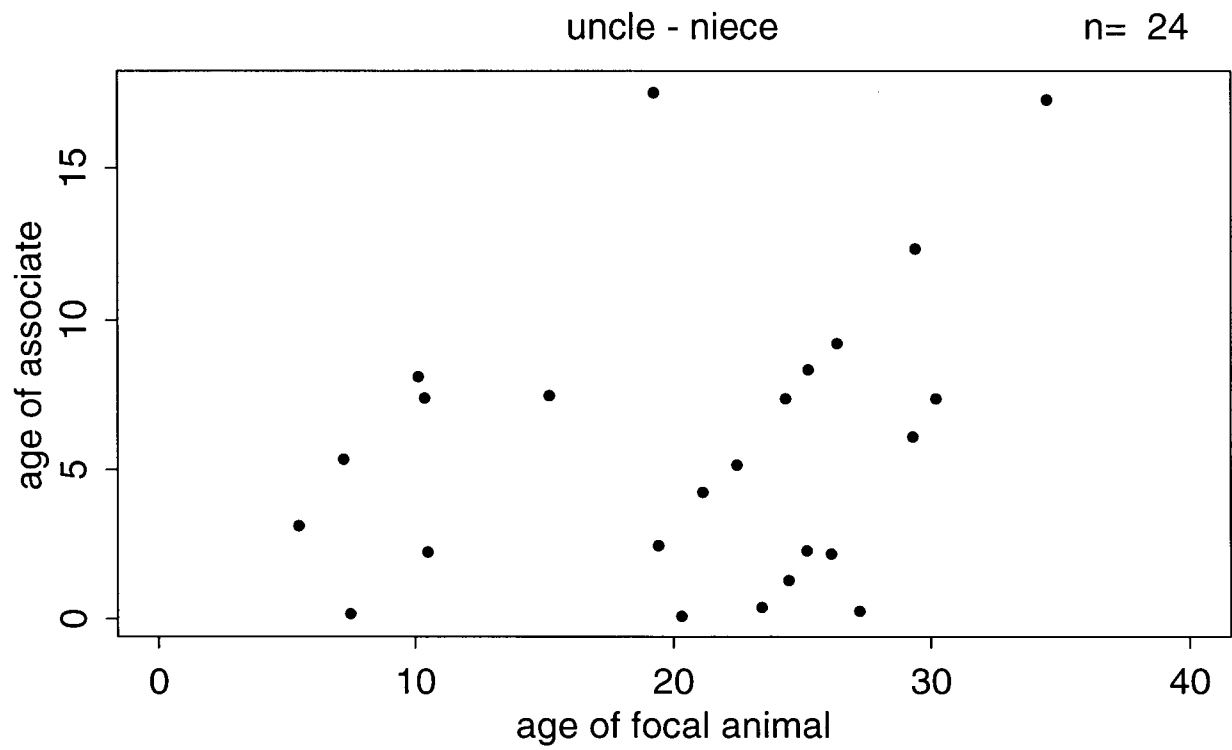
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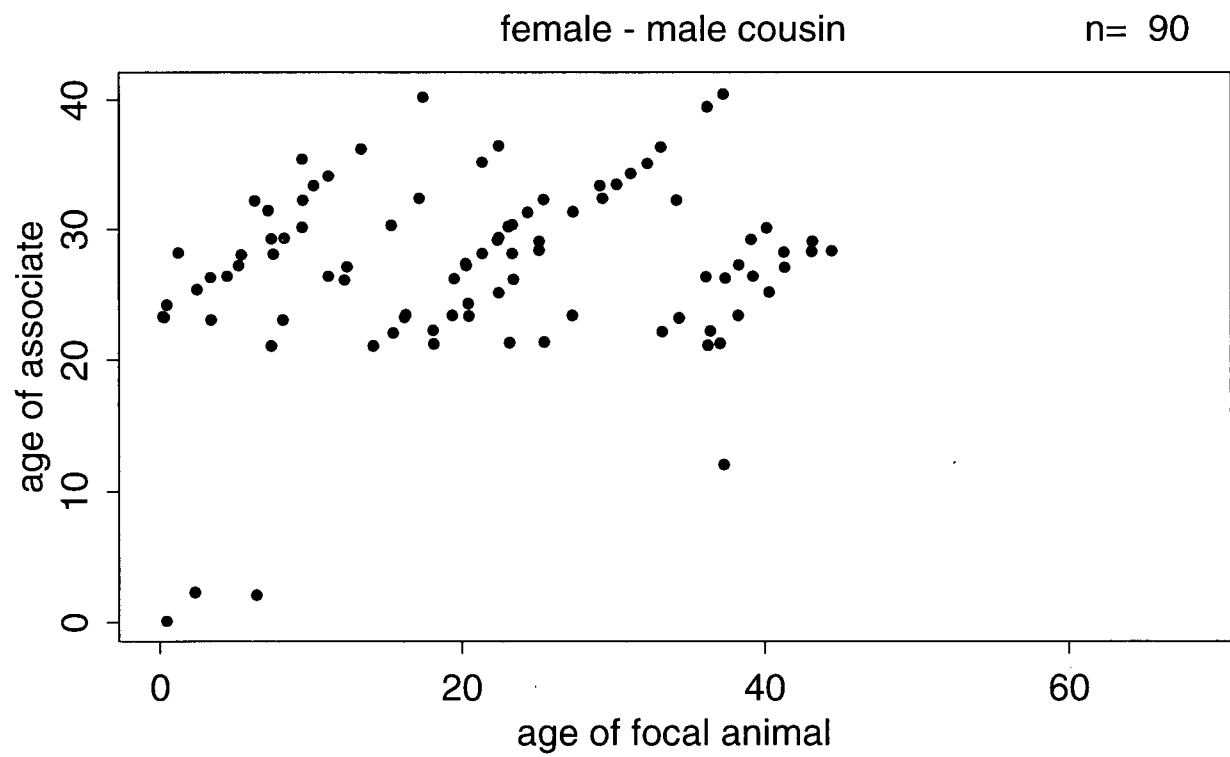
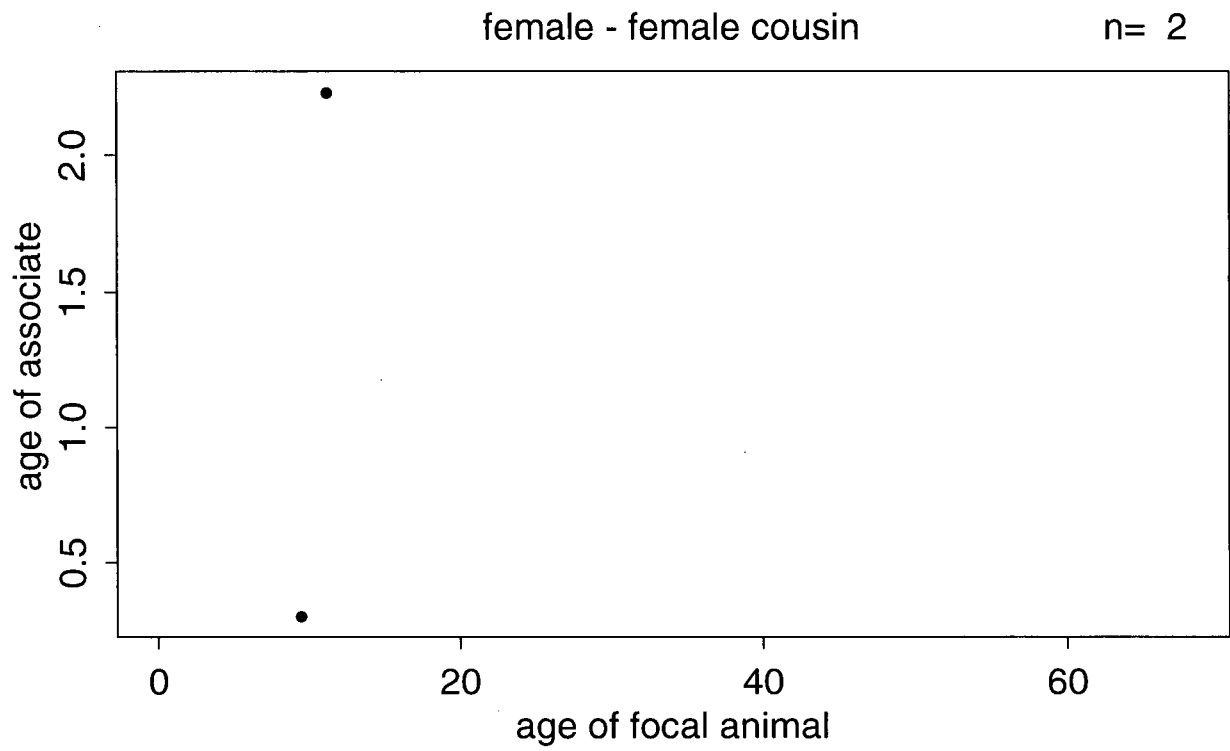
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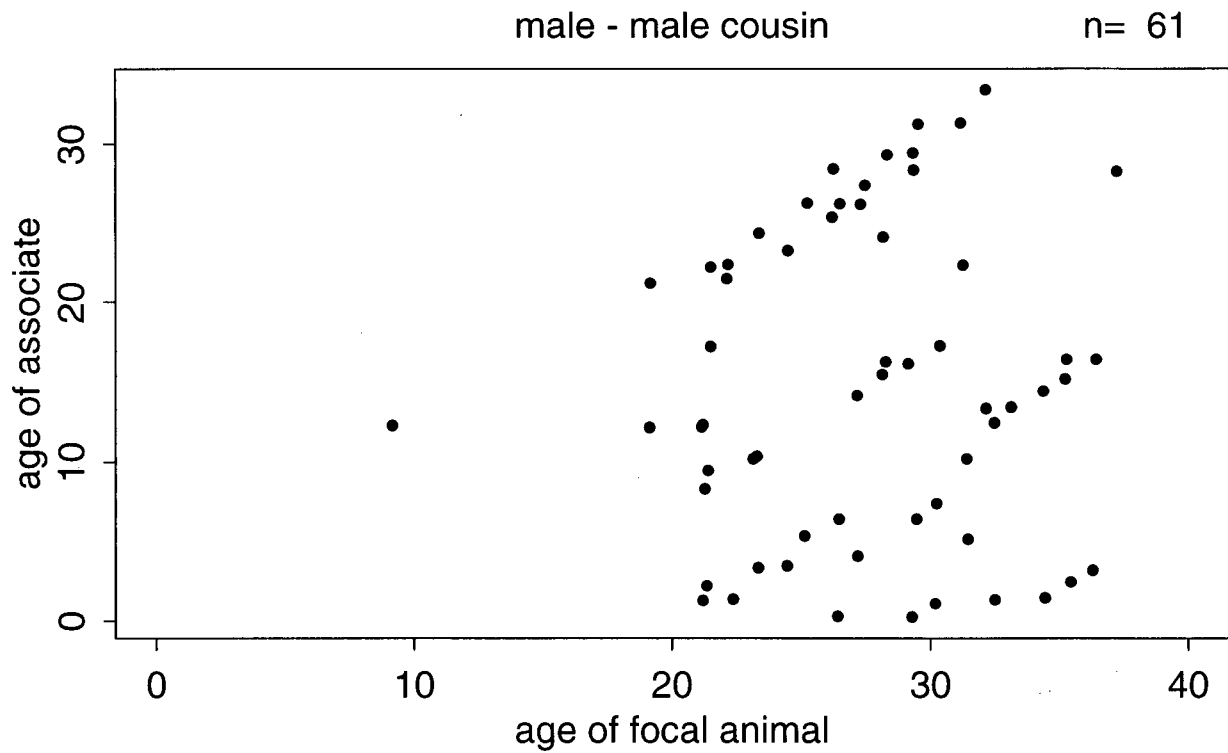
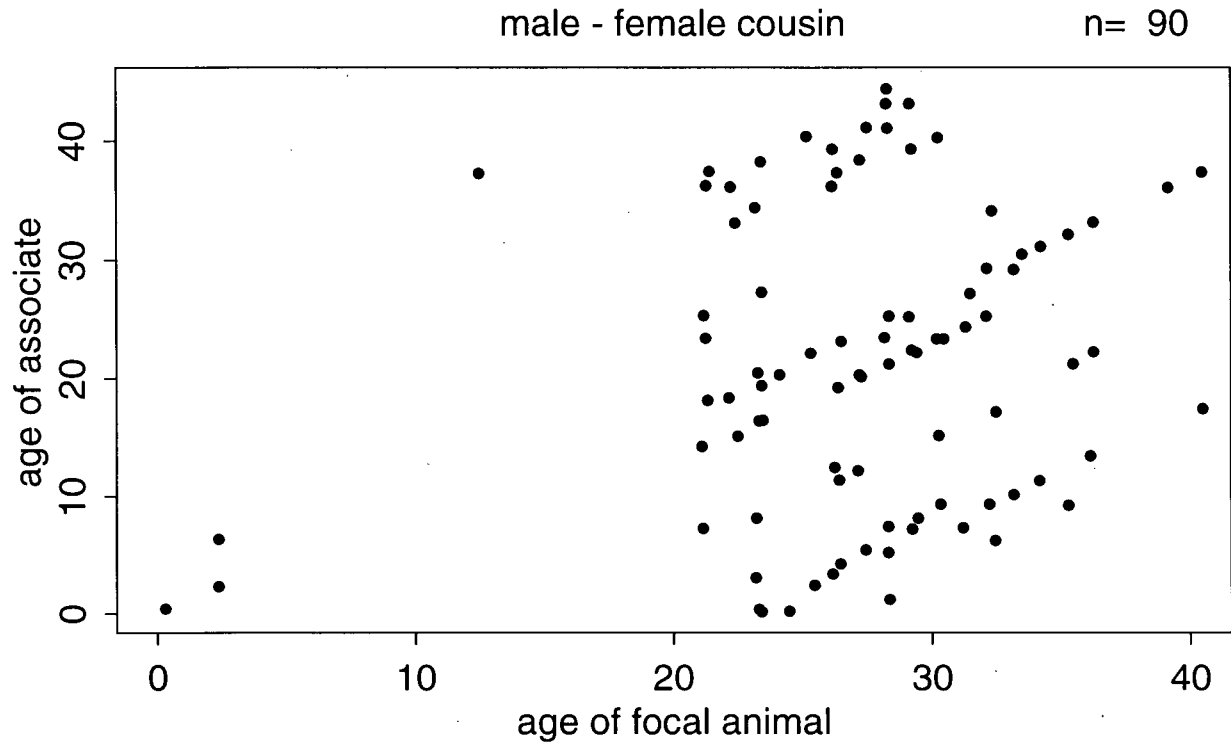
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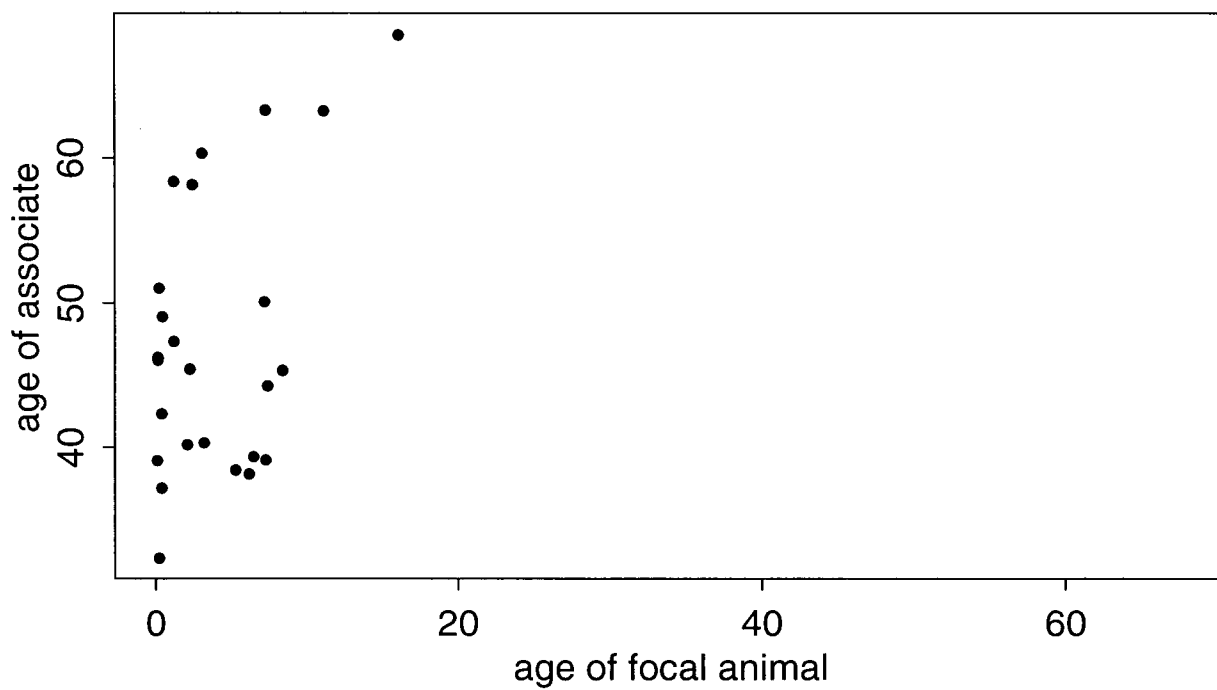
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Appendix (pair-year plots)

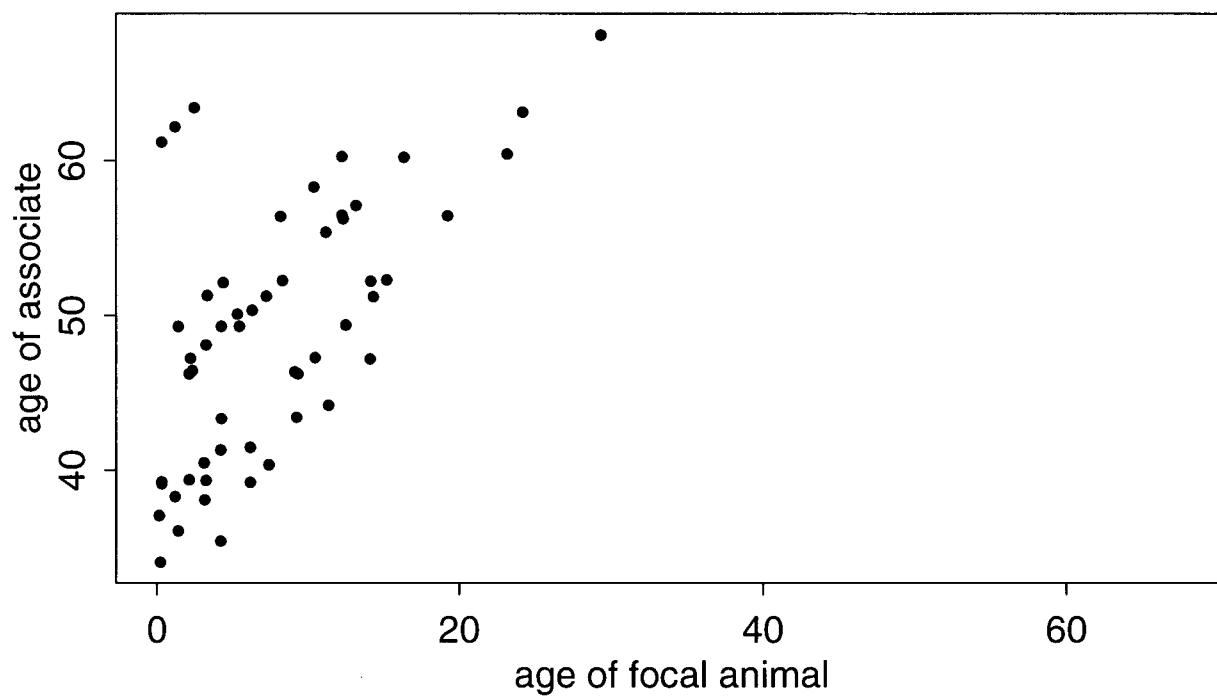
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n= 25



grandson - grandmother

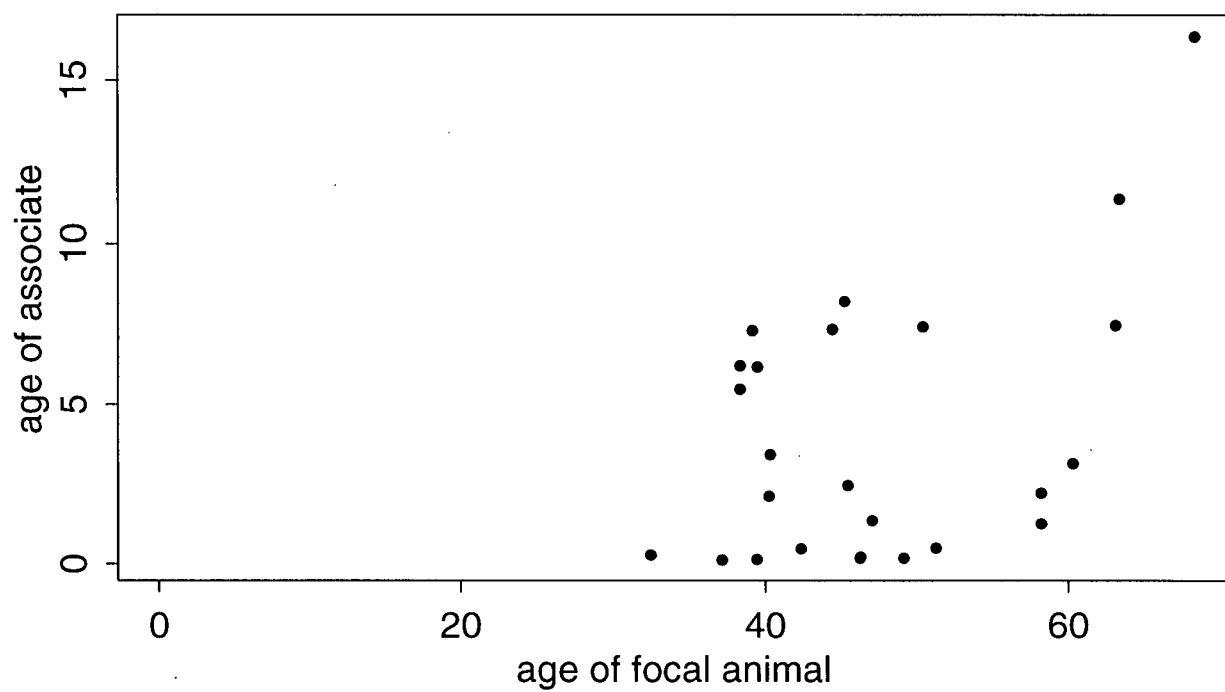
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Appendix (pair-year plots)

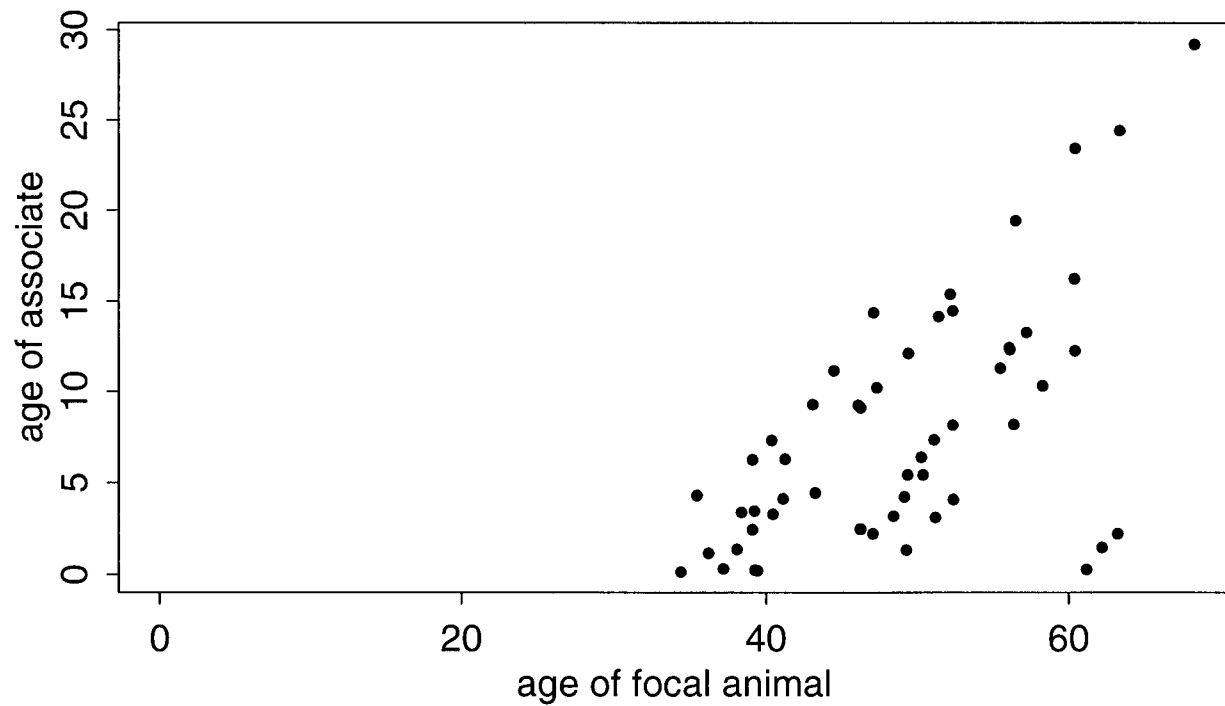
grandmother - granddaughter

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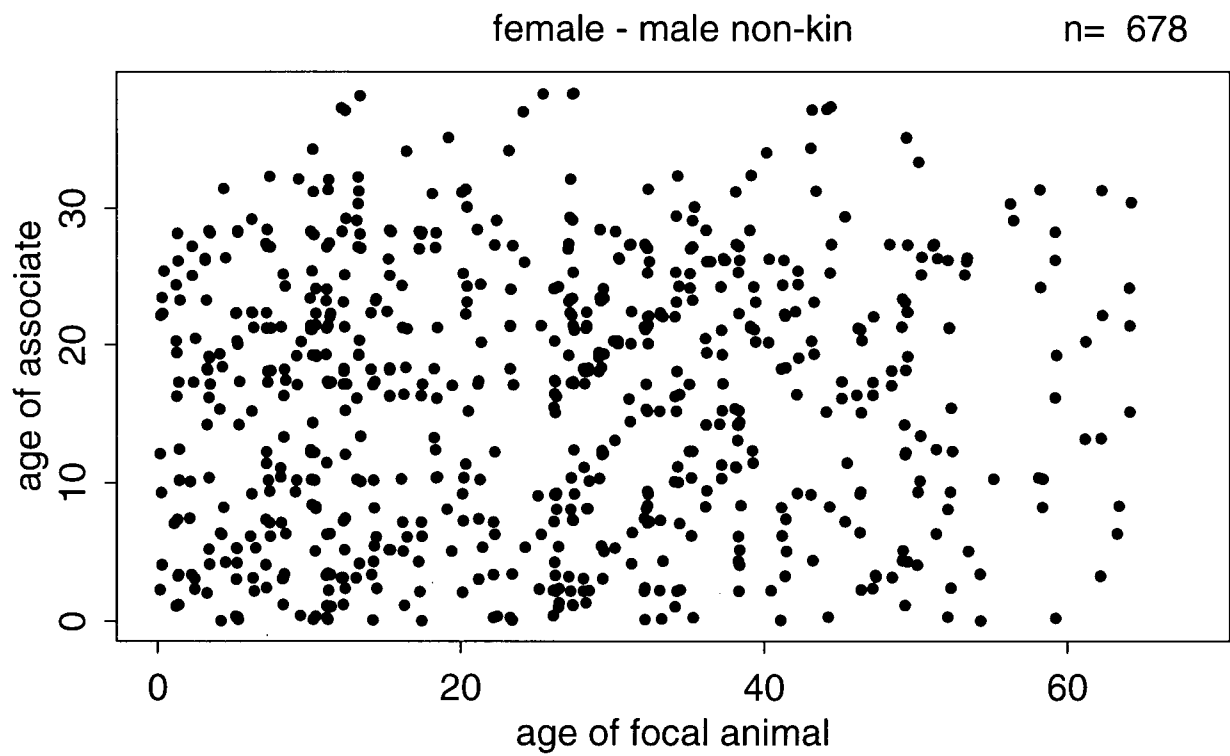
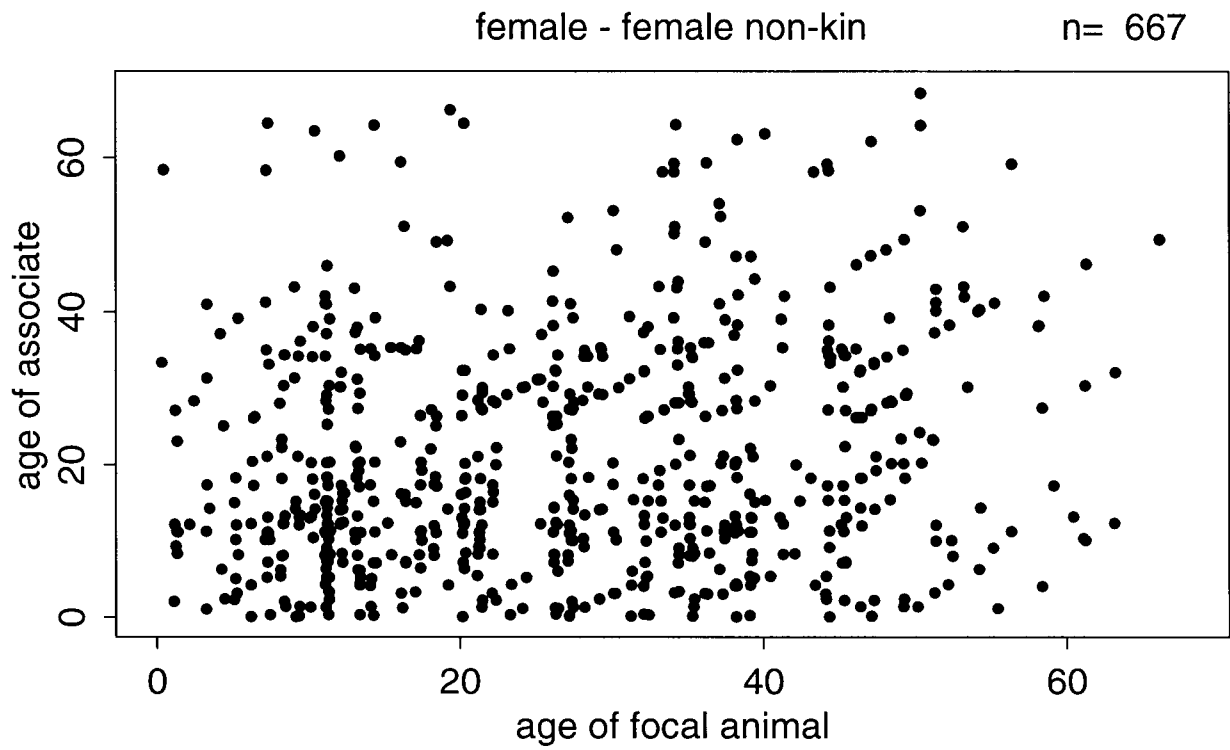


grandmother - grandson

n= 54



Appendix (pair-year plots)



Appendix (pair-year plots)

