

Survival benefits select for group living in a social spider despite reproductive costs

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Abstract

The evolution of cooperation requires benefits of group living to exceed costs. Hence, some components of fitness are expected to increase with increasing group size, whereas others may decrease because of competition among group members. The social spiders provide an excellent system to investigate the costs and benefits of group living: they occur in groups of various sizes and individuals are relatively short-lived, therefore life history traits and Lifetime Reproductive Success (LRS) can be estimated as a function of group size. Sociality in spiders has originated repeatedly in phylogenetically distant families and appears to be accompanied by a transition to a system of continuous intra-colony mating and extreme inbreeding. The benefits of group living in such systems should therefore be substantial. We investigated the effect of group size on fitness components of reproduction and survival in the social spider *Stegodyphus dumicola* in two populations in Namibia. In both populations, the major benefit of group living was improved survival of colonies and late-instar juveniles with increasing colony size. By contrast, female fecundity, female body size and early juvenile survival decreased with increasing group size. Mean individual fitness, estimated as LRS and calculated from five components of reproduction and survival, was maximized for intermediate- to large-sized colonies. Group living in these spiders thus entails a net reproductive cost, presumably because of an increase in intra-colony competition with group size. This cost is traded off against survival benefits at the colony level, which appear to be the major factor favouring group living. In the field, many colonies occur at smaller size than expected from the fitness curve, suggesting ecological or life history constraints on colony persistence which results in a transient population of relatively small colonies.

Introduction

The evolution of cooperation in animals raises the puzzling problem of how helping is maintained despite

the inherent costs associated with it. Solving this problem, which has proven one of the greatest challenges in modern biology, is central to understanding the selective forces driving the association of lower level entities into higher levels of organization (Maynard Smith & Szathmáry, 1995; Reeve & Keller, 1999). It is generally assumed that social systems form and are maintained because benefits outweigh the inherent costs of group living (Alexander, 1974). Hence, average fitness should be

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higher for individuals living in groups compared with solitary individuals. To test this prediction, a common approach of empirical studies has been to examine factors that shape reproductive success in relation to group size (Clutton-Brock, 1988; Brown & Brown, 1996; Avilés & Tufiño, 1998; Krause & Ruxton, 2002). Based on such studies, the main ecological factors invoked as responsible for the formation of groups are foraging advantages, predator defence and the establishment and maintenance of nest-sites (Alexander, 1974; Emlen, 1984; Crespi & Choe, 1997). The main genetic factor cited is inclusive fitness benefits in a broad sense (Emlen, 1984; Crespi & Choe, 1997; Griffin & West, 2003). Different factors have proved important for different species, and therefore general explanations for the evolution of group living are still lacking (Okasha, 2004; Sachs *et al.*, 2004; West *et al.*, 2006). This probably reflects the natural complexity of group living whereby multiple factors can influence fitness as a function of group size, as well as the difficulties in assessing all of the relevant fitness components because of the demographic and ecological constraints inherent in whole-organism studies.

Group living invariably entails costs, in particular those involving competition for resources and conflict over reproduction (Alexander, 1974; Hamilton & May, 1977; Choe & Crespi 1997). A number of other disadvantages such as increased parasitic load, brood parasitism and attraction of predators, to mention a few, vary with breeding unit size and contribute to the net cost of group living (Brown & Brown, 1996). Although the numerous environmental and genetic costs and benefits of group living may be unknown or difficult to quantify, it is possible to determine the combined effects of these factors on fitness and its components, by examining the relationship between average individual lifetime reproductive success (LRS) and group size (Clutton-Brock, 1988; Brown & Brown, 1996; Avilés & Tufiño, 1998). Such studies have been developed in long-lived iteroparous species by partitioning LRS into several components: (1) survival to breeding age; (2) reproductive life span; (3) average fecundity during the reproductive life span; (4) offspring survival until reproductive age (Brown, 1988; Clutton-Brock, 1988). Per capita productivity or survival in relation to colony size have been widely studied in social insects (e.g. Bourke & Franks, 1995), but comprehensive empirical data on the effect of group size on a suit of fitness components comprising LRS exist for only a few species (acorn woodpeckers, Koenig, 1981; groove-billed anis, Vehrenkamp *et al.*, 1988; cliff swallows, Brown & Brown, 1996; theridiid social spiders, Avilés & Tufiño, 1998; long-tailed macaques, van Noordwijk & van Schaik, 1999; mice, Gerlach & Bartmann, 2002).

Social spiders are well suited for exploring costs and benefits of group living and how these opposing selective forces interact to determine overall fitness (Avilés & Tufiño, 1998). They form colonies that range from a few

to hundreds of individuals and have a relatively simple demographic structure (Avilés, 1997). Social spider colonies are founded by inseminated females that exhibit two substantially different types of dispersal, 'propagule dispersal' where one to a few females and their brood initiate a colony and 'fission' where multiple females – usually closely related (see below) – bud off from an existing colony. These strategies correspond to potentially long-range dispersal or emigration and short-range colony budding or translocation, respectively (Vollrath, 1982; Avilés, 2000). Unlike the social insects, mating takes place within the colony among close relatives, as premating dispersal is eliminated (Avilés, 1997). The spiders are relatively short lived (from a few months to a couple of years, depending on the species), whereas colonies may persist for several generations. Generations within the colonies are usually discrete (Avilés, 1997). This suite of life history traits makes it possible to quantify the average LRS of females in each generation as a function of colony size by determining the number of adult offspring produced by females in colonies of different sizes. The prediction that the benefits of group living outweigh costs would be met if LRS were greater for females living in groups than solitarily. Avilés & Tufiño (1998) showed that in the neotropical social spider *Anelosimus eximius* (Theridiidae) females suffer a reduced probability of reproduction, but an improved likelihood of colony and offspring survival as the size of their colonies increases. The net effect of this cost/benefit structure was an individual fitness curve that was at a maximum at intermediate colony sizes.

Similar to many of the social vertebrates, social spiders are cooperative breeders, there are no sterile castes but there can be nonreproducing individuals that may invest heavily in provisioning offspring (Salomon & Lubin, 2007; Lubin & Bilde, 2007). Sociality in spiders has evolved repeatedly, with phylogenetic evidence suggesting as many as 18 independent origins in seven spider families (Avilés, 1997; Agnarsson *et al.*, 2006; Johannesen *et al.*, 2007). Such evidence supports the origin of group living in spiders via the subsocial route, through philopatry and elimination of dispersal in species characterized by extended maternal care (Kullman, 1972; Buskirk, 1981; Kraus & Kraus, 1988; Avilés, 1997; Agnarsson *et al.*, 2006). The subsocial route is also one of the proposed pathways to eusociality in insects (Queller, 1992) and is parallel to the formation of family groups in cooperatively breeding birds and mammals (Emlen 1984). Common to the social spiders, but in contrast to most social insects and vertebrates, except for the naked mole rats (Reeve *et al.*, 1990), mating takes place among colony members (siblings or cousins) which results in high levels of inbreeding (Riechert & Roeloffs, 1993; Avilés, 1997; Lubin & Bilde, 2007). Such inbreeding is expected to incur fitness costs through the loss of heterozygote advantage and, at least initially, the expression of deleterious recessive alleles (Charlesworth &

Charlesworth, 1987), although the latter should be purged for the most part by repeated inbreeding (Barrett & Charlesworth, 1991). Selective factors promoting group living and intra-colony mating could be ecological constraints on dispersal and colony founding (Avilés & Gelsey, 1998; Bilde *et al.*, 2005) and substantial direct and indirect fitness benefits to counter the costs of inbreeding and competition among kin within groups (Hamilton & May, 1977). Intra-colony mating and inbreeding simultaneously increases relatedness, which might increase inclusive fitness benefits, promote cooperation and reduce conflicts (West-Eberhard, 1975).

Here we explore the net fitness consequences of group living in the African social spider *Stegodyphus dumicola* Pocock 1898 (Eresidae). In field studies, we investigated the effect of colony size on fecundity, reproduction and survival and how these fitness components interact to form the overall fitness function in relation to colony size. Within two study populations, we studied a natural range of colony sizes, including single founding females, and estimated five components of survival and reproduction as a function of colony size. These components included probability of female reproduction, three measures of within-colony survival (juvenile, subadult and adult survival), and between-generation colony survival, which overall constitute female LRS. We used these fitness components to model LRS as a function of colony size, and used this function to investigate whether colonies in the field occur at optimal group sizes.

Materials and methods

Study organism

Stegodyphus dumicola is one of three social species of the genus *Stegodyphus* inhabiting dry thorn bush savannah in Southern Africa (Kraus & Kraus, 1988). It is an annual species with discrete generations that form sessile aerial colonies varying in size from a single female with offspring up to several hundred individuals. New colonies are founded by inseminated females that disperse short distances by foot, or larger distances by ballooning (Seibt & Wickler, 1988a; Schneider *et al.*, 2001). Colony growth is presumed to occur mainly via intra-colony mating (Avilés, 1997; Lubin & Bilde, 2007). Colony turnover is high (Henschel, 1998) and surviving colonies persist up to six years until they go extinct or proliferate (Lubin & Crouch, 2003). Genetic analysis of mtDNA reveals that approximately 86% of the colonies are monomorphic, suggesting predominantly single lineage foundation of one or several related females and little gene flow between colonies (Johannesen *et al.*, 2002). Nonetheless, recent genetic analysis of the whole genome using AFLP fingerprinting revealed sufficient genetic variation to suggest occasional gene flow between colonies (D. Smith personal communication), perhaps by ballooning females

dispersing between colony clusters (Schneider *et al.*, 2001).

In our study areas in Namibia, the females reproduce in the summer months of February–April and care for the young by regurgitation feeding and sharing prey until the onset of winter in May, when they are consumed by the young (Seibt & Wickler, 1987). Colonies with juveniles are inactive through winter (May–September). Colony activity resumes in September/October.

Study sites

Two geographically distinct populations separated by the central highlands of Namibia were selected for this study: One population was studied from January to December 2003 in the area surrounding Rooisand Desert Farm, 170 km south-west of Windhoek towards Walvis Bay. A second population was studied from December 2003 to November 2004 at Oupembamewa Cattle Farm, close to Seeis, 60 km East of Windhoek. The Rooisand area is a dry savannah harbouring a low-density population of *S. dumicola* at the edge of the species' range, which is limited by the Namib desert. Oupembamewa is more humid and more densely vegetated (Barnard, 1998; Mendelsohn *et al.*, 2002), and *S. dumicola* colonies occur in higher densities (Table 1). Voucher specimens from both locations were deposited at The National Museum of Namibia.

Fitness components

For semelparous organisms, such as *S. dumicola* (Seibt & Wickler 1987), individual fitness can be obtained by using the rate-insensitive individual fitness estimate LRS (Brommer *et al.*, 2004). LRS can be broken down into components of survival and individual reproduction (Brown *et al.*, 1990; Avilés & Tufiño, 1998). In this study LRS was divided into five components: (a) R1, young/female; (b) S1, colony survival between breeding seasons; (c) S2, survival from egg to the end of maternal care; (d) S3, survival from the end of maternal care to the subadult stage and (e) S4, survival from subadult to reproduction. It should be noted here that S4 includes adult dispersal events as well as mortality.

Data for the life history components were obtained using several data sets (see Table 2) as it was not possible to obtain complete data for all components of LRS from a single sample of colonies. Colony size, measured as the number of reproducing females (a continuous number), can be determined in the field only by destructively taking the colony apart and counting individuals. Colonies that are opened to count individuals cannot be re-established in the field and are therefore unavailable for repeated observations. Within each population, we used one set of colonies to determine colony survival (S1) in the field by individually marking and surveying these colonies over a period of 12 months. Reproduction (R1)

Table 1 Comparison of geographical and biological characteristics of the two study sites.

	Rooisand	Oupembamewa
Research areas	Desert game farm	Cattle farm
Altitude farm house (m)	1156	1664
Coordinates	23°17'S, 16°06'E	22°33'S, 17°34'E
Average annual temperature (°C)	18–20	18–20
Average maximum hottest month (°C)	30–32	30–32
Average minimum coldest month (°C)	4–6	2–4
Water deficit (mm year ⁻¹)	1900–2100	1700–1900
Annual rainfall (mm)	200–250	350–400
Vegetation type	Savannah transition to semi desert	Highland savannah
Vegetation structure	Sparse shrubland	Dense shrubland
Landscape name	Western-central escarpment	Khomas Hochland
Average plant production	Low–medium	Medium–high
Remarks	No grazing by cattle, dense grass coverage, few shrubs, scattered acacia trees	Intensive grazing pressure by cattle, Hartebeest & Kudu. Degraded grass coverage, mainly small to medium shrubs

Table 2 Collection dates, the number of colonies used, and data used from colonies at Rooisand and Oupembamewa used to estimate components of lifetime reproductive success.

	Rooisand	Oupembamewa
Size distribution	Colonies: $n = 104$ Surveyed February 2003	Colonies: $n = 595$ Founding colony: $n = 93$; Daughter colony $n = 280$; Isolated colonies: $n = 222$. Surveyed December 2003
R1, Clutch size and hatching success	Egg sacs: $n = 75$ From colonies collected February–May 2004 (21 colonies) and December 2004 (11 colonies)	Egg sacs: $n = 152$ From colonies collected May 2004 (14 colonies) and November 2004 (12 colonies)
Female size	Female: $n = 92$ Collected December 2004 (12 colonies)	Females: $n = 125$ Collected May 2004 (14 colonies)
S1, survival between reproductive seasons	Colonies: $n = 96$ Surveyed regularly from January to December 2003	Colonies: $n = 63$ Surveyed regularly from January to November 2004
S2, survival from egg to end of maternal care	Colonies: $n = 21$ Collected February–May 2003	Colonies: $n = 14$ Collected May 2004
S3, survival from end of maternal care to sub-adult	Colonies: $n = 32$ Collected February–May 2003 ($n = 21$) and December 2003 ($n = 12$)	Colonies: $n = 26$ Collected May 2004 ($n = 14$) and November 2004 ($n = 12$)
S4, survival from subadult to maternal care	Colonies: $n = 69$ Collected in December 2002 (48 colonies) and May 2003 (21 colonies)	
Colony volume vs. number of females	Colonies: $n = 10$ Collected December 2003	Colonies: $n = 44$ Measured in May and collected in May 2004 and November 2004
Colony size class vs. number of females	Colonies: $n = 32$ Collected February–May 2003 and December 2003	Same colonies as above. Divided into size classes using partition analysis
Colony volume vs. size class	Colonies $n = 18$ Collected Dec 2003 Divided into size classes using partition analysis	

was determined as the average number of young per female based on the number of hatched eggsacs and clutch size in relation to the number of females in the

colony using a separate set of colonies. Individual survival (S2 and S3) was estimated as the proportion of surviving offspring before onset of winter (May) and after

winter (November) in two separate sets of colonies using predicted values of initial number of offspring estimated from reproductive data (R1). Survival from subadult to reproduction (S4) was obtained for only one population (Rooisand) from one additional set of colonies (Table 2). As our measure of colony size, we use the number of reproducing females in a colony. This is derived from the relationship between physical dimensions of a colony (in cm^3) and the number of females found within the colony, allowing us to relate the fitness measures taken at different life stages to a single common unit of measurement, which is absolute number of reproducing females (see below).

Definition of colony size

For R1, S2 and S3 colony size was estimated from the number of exoskeletal remains of adult females found in the nest's brood chambers. Although not all females within a colony reproduce because of intra-colony competition for resources, all females – those that reproduced and those that did not – are consumed by the young (Seibt & Wickler, 1987; Henschel *et al.*, 1995; Salomon & Lubin, 2007). The number of female exoskeletons therefore represents the total number of females in the maternal generation, and R1 is then estimated as the number of young/female in relation to colony size.

For the probability of colony survival (S1) we estimated the proportion of colonies of different size classes that survived to the next reproductive season. Colonies were classified in size classes based on nest volume, with nest volume calculated as an ellipsoid based on measures of nest length, width and height. S1 was estimated for nest size classes because multiple nests of approximate same size class were needed to estimate proportions of survival. The number of reproducing females corresponding to each nest size class was separately derived by linear regression based on the relationship between nest volume and number of females in a separate sample of nests (Table 3). To estimate this relationship, nests were carefully taken apart and the number of dead females was counted. Nest volume is linearly related to the number of individuals in the colony (Henschel, 1993), as we also found in our study.

Data collection and estimates of LRS components: reproduction R1

R1 (average number of young/female) was calculated as the product of the proportion of hatched egg sacs times the total number of eggsacs per female times average clutch size in colonies of different sizes. Clutch size was determined by counting the eggs from unopened egg sacs

Table 3 The relationship between different colony size estimates. (a) Linear regression of nest volume on colony size for Rooisand ($n = 10$) and Oupembamewa ($n = 44$). (b) Relationship between size classes, number of females and volume in Rooisand; the mean number of females differed between size classes (Welch ANOVA, $F_2 = 18.1047$, $P = 0.0013$). (c) In Oupembamewa, colonies were divided into size classes based on partition analysis of the relationship between the number of females and nest volume ($r^2 = 0.364$).

		R^2	d.f.	F -ratio	Prob > F
(a) Nest volume as a function of colony size					
Rooisand	$\ln(y) = 5.75 + 0.62 \cdot \ln(x)$	0.49	1.8	7.6641	0.0244
Oupembamewa	$\ln(y) = 3.64 + 0.82 \cdot \ln(x)$	0.51	1.42	44.6972	< 0.0001
		No. females, mean (95% confidence interval)	Corresponding volume (in November) (95% confidence interval)	No. of juveniles in May (range)	No. of subadults in November (range)
(b) Rooisand					
Single	1	(-209–855.1) $n = 5$	(18–73) $n = 10$	(18–55) $n = 5$	
Small	3.69 (2.72–4.66) $n = 19$	(140–827.0) $n = 12$	(12–211) $n = 10$	(11–175) $n = 11$	
Medium	14.14 (8.69–19.60) $n = 7$	(1582–2956.8) $n = 3$	(176–566) $n = 4$	(48–241) $n = 3$	
Large	33.00 (15.65–50.35) $n = 6$	(311–1685.2) $n = 3$	(198–608) $n = 4$	(57–108) $n = 3$	
(c) Oupembamewa ($n = 44$)					
		No. females		Corresponding volume in May	
		Median	Interval		
Small	1	1		< 54 cm^3	
Small medium	4	2–6		54–188 cm^3	
Medium	9.5	7–12		188–312 cm^3	
Large medium	14	13–15		312–370 cm^3	
Large	18	16–20		370–462 cm^3	
X-large	24	21–27		> 462 cm^3	

from colonies of different sizes (Table 2). The proportion of hatched eggsacs was the ratio of hatched to unhatched eggsacs in relation to colony size.

Female body size may be influenced by colony size because of intra-colony competition and may also covary with clutch size. Therefore, we investigated the relationship between female body size and colony size by measuring prosoma width of female exoskeletons with a digital caliper, accurate to 0.01 mm in a sample of colonies from each location (Table 2). For each location, the relationships between female size and colony size and between female size and clutch size were analysed with linear regressions. The effect of location (Rooisand and Oupembamewa) on clutch size and female size was analysed with ANOVA with colony size nested within location. The effect of location and colony size on the ratio of hatched egg sacs/female was analysed with ANCOVA. All statistical analyses were performed using JMP version 5.1.2. (© SAS Institute Inc. 1989–2004).

Colony survival between reproductive seasons, S1

In Rooisand, 55 single female, 20 small, 14 medium and 7 large colonies (based on volume) were surveyed monthly throughout the year from January to December 2003 when survival was recorded. In Oupembamewa, 6 small, 17 small-medium, 15 medium, 9 medium-large, 8 large and 8 extra-large colonies were surveyed from January to November 2004. In both cases, S1 was calculated as the percentage of colonies within each size class surviving until the following reproductive season.

Offspring survival from egg to the end of maternal care, S2

Survival from egg to the end of maternal care, S2, was calculated as the ratio between the number of juveniles seen alive in a set of colonies collected during the period with maternal care (February–May, Table 2) and the number of spiders expected to have been produced in those nests. The latter figure was calculated from the number of hatched egg sacs found in a colony multiplied by the average clutch size for colonies of that size at a given locality (Fig. 1).

Juvenile Survival from the End of Maternal Care to Sub-adult, S3

S3 was estimated in a separate set of colonies as the relationship between the observed number of subadult spiders in November (after winter) and the number of juveniles expected to have been present in those nests in May (before winter). The latter quantity was inferred for each locality from the size of each nest using the previously estimated R1 and S2 relationships (see above).

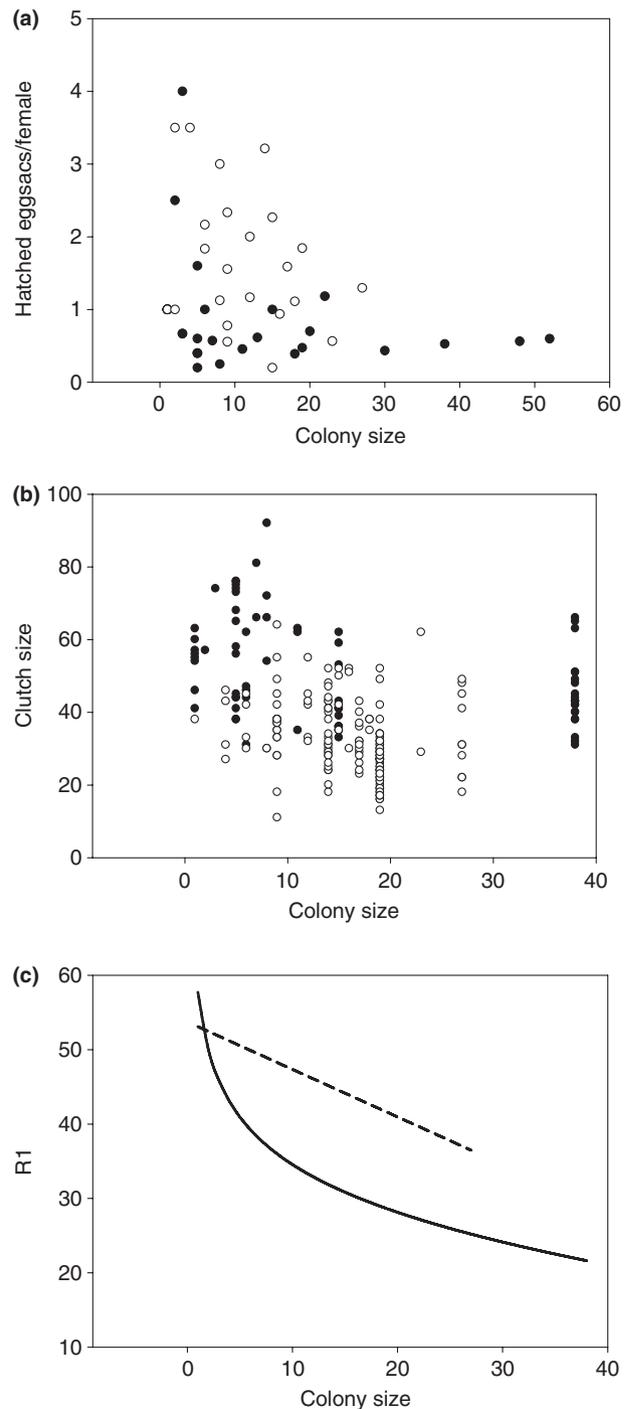


Fig. 1 Reproduction in relation to colony size: (a) The ratio of hatched egg sacs per female and (b) Clutch size per female in relation to colony size for Rooisand (●) (—) and Oupembamewa (○) (- - -). (c) R1, young per female in relation to colony size.

The ratio of observed subadults (November) to expected juveniles (May) was then regressed on colony size to obtain S3 as a function of colony size.

Survival from subadult to egg production, S4

S4 includes adult dispersal events as well as mortality between the subadult and reproducing stage. S4 was calculated in Rooisand only by comparing average number of spiders in colonies of three size classes (small, medium, large) in December 2002 with the number of females found in colonies of similar size classes in May 2003. These data were not available for Oupembamewa, so to obtain comparable measures of LRS for the two sites (see below), S4 from Rooisand was used in the calculation of LRS for both populations. As Rooisand is a drier and harsher habitat than Oupembamewa and survival therefore is likely to be lower in Rooisand, we may have underestimated S4 in Oupembamewa. As a consequence, LRS is likely a conservative estimate compared with that of Rooisand, and thus LRS in Oupembamewa may be underestimated.

Lifetime reproductive success in relation to colony size

Lifetime reproductive success was calculated by multiplying the fitness components R1, S1, S2, S3 and S4, where S2, S3 and S4 are measures of within-colony survival given that a colony had survived the respective time period. The probability of whole colony survival between reproductive seasons was accounted for by multiplying with S1. Even though most components of LRS were calculated for a continuous range of colony sizes, S1 can only be calculated for discrete colony size classes because multiple colonies of similar size were needed to estimate the proportion surviving. Therefore, to be consistent, we present the composite measure of LRS as a function of discrete size classes of colonies ranging from 1 to 38 females. These colony sizes are comparable with those reported by Henschel (1993), who showed that most reproducing colonies (March)

contained < 20 adult females. Subsequently, we used the linear relationship between colony volume and colony size, measured as the number of reproducing females, to model the predicted fitness return curve of LRS as a function of colony size.

Size distribution of colonies in the field

The colony-size dependent LRS provides predictions of the colony sizes at which mean individual fitness should be maximized. We determined colony size distributions in our two study populations to compare whether field colonies are distributed following the predicted patterns. We assessed colony size distribution from 104 colonies observed in Rooisand in February 2003 and 596 colonies observed in Oupembamewa in November/December 2003. As a consequence of colony foundation by budding from existing colonies, often colonies occur in clusters on the same bush; in these clusters we could identify by its size and condition which nest (the founding nest) gave rise to new colonies (daughter nests). In Oupembamewa we recorded whether colonies occurred as isolated nests (propagule founding) or in clusters, and in the latter case we identified their status as founding nest or daughter nest (founded by colony fission) and calculated the proportion of nests that gave rise to daughter colonies.

Results

Reproduction

Clutch size decreased with increasing colony size in both Rooisand and Oupembamewa (Table 4a and Fig. 1a). Clutch size was significantly larger in Rooisand (mean = 52.12 eggs/egg sac, SD = 14.02, $n = 75$) than it was in Oupembamewa (mean = 32.5 eggs/egg sac, SD = 10.19, $n = 152$) (nested ANOVA $F_{32,226} = 9.29$, $P < 0.0001$; effect of location, $F = 77.99$, $P < 0.0001$; effect of colony

Table 4 Linear relationship of (a) clutch size as a function of colony size; (b) female size as a function of colony size; (c) clutch size as a function of female size; (d) hatching success of egg sacs in relation to colony size; Data have depicted in Fig. 1.

		r^2	d.f.	F-ratio	Prob > F
(a) Clutch size as a function of colony size					
Rooisand	$y = 56.85 - 0.35x$	0.13	1.73	10.8292	0.0015
Oupembamewa	$y = 40.10 - 0.48x$	0.06	1.150	9.9590	0.0019
(b) Female size as a function of colony size					
Rooisand	$y = 2.70 - 0.0044x$	0.06	1.90	6.2012	0.0146
Oupembamewa	$y = 2.54 - 0.0099x$	0.10	1.123	14.0879	0.0003
(c) Clutch size as a function of female size					
Rooisand	$y = -16.02 + 25.97x$	0.15	1.74	12.2513	0.0008
Oupembamewa	$y = -35.23 + 28.91x$	0.08	1.102	9.2656	0.0030
(d) Ratio of hatched to unhatched egg sacs as a function of colony size					
Rooisand, February–May	$\ln(y) = -0.060 - 0.16 \ln(x)$	0.44	1.19	15.17	0.0010
Rooisand, December	$\ln(y) = -0.341 - 0.29 \ln(x)$	0.51	1.10	10.56	0.0087
Oupembamewa May	$\ln(y) = -0.002 - 0.14 \ln(x)$	0.53	1.12	13.58	0.0031
Oupembamewa, November	$\ln(y) = -0.171 - 0.05 \ln(x)$	0.01	1.10	0.11	0.74

size nested within location, $F = 3.73$, $P < 0.0001$; effect of sampled colony nested within colony size and location, $F = 1.01$, $P = 0.42$). The number of hatched egg sacs per female was significantly larger in Oupembamewa [mean = 1.34, 95 % confidence interval (1.03; 1.74)] than in Rooisand [mean = 0.74, 95% confidence interval (0.60; 0.91)]; (ANCOVA $F_{3,57}P = 0.0012$; effect of location $F = 14.80$ $P = 0.0003$; effect of colony size $F = 1.5547$ $P = 0.2178$; the interaction effect of location \times colony size: $F = 1.4223$, $P = 0.2382$). The number of hatched egg sacs per female in Rooisand decreased with increasing colony size ($\ln(y) = 0.021 - 0.20 \ln(x)$; $R^2 = 0.18$, $F_{1,31} = 6.80$ $P = 0.0141$), whereas in Oupembamewa there was no consistent relationship (Fig. 1b). R1 was calculated as the number of hatched young produced per female as a function of colony size. R1 decreased with increasing colony size in both Rooisand and Oupembamewa (Fig. 1c).

Female size decreased with increasing colony size (Table 4b); and females from Rooisand were significantly larger than females from Oupembamewa (nested ANOVA $F_{25,216} = 6.21$, $P < 0.0001$; effect of location, $F = 36.72$, $P < 0.0001$; effect of colony size nested within location, $F = 5.38$, $P < 0.0001$; effect of sample colony nested within colony size and location, $F = 0.87$, $P = 0.52$). There was a positive linear relationship between clutch size and female size (prosoma width) in both locations (Table 4c). The proportion of eggsacs that hatched was negatively correlated with colony size (Table 4d).

Survival

For both locations, colony survival increased dramatically with colony size (Table 5, Fig. 2). S1 was significantly lower for single female colonies compared to larger colonies (Rooisand, Likelihood ratio: $X^2_{2,93} = 18.050$ $P = 0.0004$), in Oupembamewa, S1 was the highest for intermediate sized colonies (Likelihood ratio: $X^2_{2,60} =$

Table 5 The probability of survival between reproductive seasons (S1) of colonies in discrete size classes in Rooisand and Oupembamewa.

Colony size	No. females	<i>n</i>	<i>P</i> (survival)
Rooisand			
Single	1	55	0.09
Small	4	20	0.50
Medium	14	14	0.43
Large	33	7	0.43
All colonies		96	0.25
Oupembamewa			
Small	1	6	0
Small medium	4	17	0.29
Medium	9.5	15	0.53
Large medium	14	9	0.67
Large	18	8	0.63
X-Large	24	8	0.38
All colonies		63	0.43

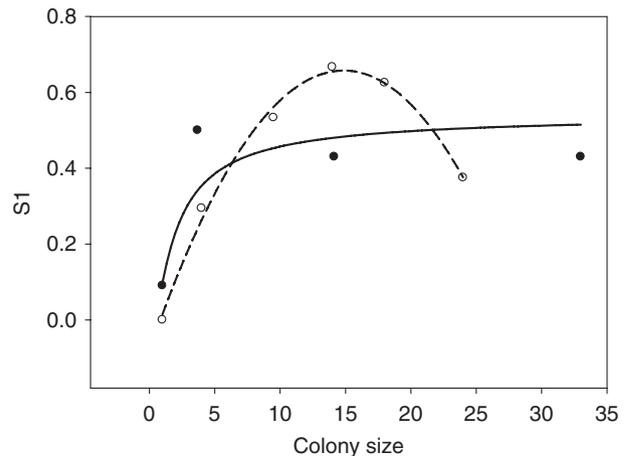


Fig. 2 S1, survival of the colonies between seasons in relation to colony size for Oupembamewa (○) $n = 63$ or Rooisand (●) $n = 96$. Each point represents the percentage of colonies that survived for 1 year (Table 5).

12.094, $P = 0.0335$). In contrast, the survival of juveniles within the colonies (S2) decreased with colony size in both locations (Table 6, Fig. 3). The survival of young until the subadult stage (S3) improved with colony size in Oupembamewa, but showed little change in Rooisand (Table 7, Fig. 4). Estimates of S2 and S3 were based on data given in the Appendix. The probability of survival from the subadult to the reproductive stage (S4) increased with colony size. This number was estimated as the proportion of adult reproducing spiders surviving between November and February in colonies of three size categories at Rooisand: Small (estimated number of adult females 3.2; $n = 24$) survival = 0.06; Medium (17.5 adult females, $n = 17$) survival = 0.286; Large (38 adult females, $n = 30$) survival = 0.377.

Lifetime reproductive success

The relative values of the five components of LRS, R1, S1, S2, S3 and S4 (S4 only for Rooisand) in relation to colony size are depicted in Fig. 5. For each component the highest value was set to 1 and the other values scaled relative to the highest value to illustrate these four components on the same scale and thus allow a visual comparison of the effect of group size on each fitness component. A model of average individual LRS in relation to colony size was obtained by multiplying these five fitness components ($R1 \times S1 \times S2 \times S3 \times S4$) (Fig. 6). The model indicated an increase in LRS with increasing colony size for both populations. LRS was much lower in the Rooisand population than in Oupembamewa. In Rooisand, LRS increased with increasing colony size until a colony size of approximately 15 females and stabilized at a very low LRS < 1 . In Oupembamewa, LRS was considerably higher with a

Table 6 The linear relationships between the number of observed juvenile spiders at the end of the maternal care period as a function of colony size (1A and B), and of expected number of juveniles at this time as a function of colony size (2A and 2B, see also Appendix Fig. A1). S_2 , the probability of offspring survival from egg to the end of maternal care in relation to colony size, was calculated by dividing equation 1A/2A for Rooisand and equation 1B/2B for Oupembamewa (Fig. 3).

		R^2	d.f.	F-ratio	Prob > F
No. juvenile spiders as a function of colony size					
1A Rooisand	$\ln(y) = 3.45 + 0.71 \cdot \ln(x)$	0.82	1.19	88.41	0.0001
1B Oupembamewa	$\ln(y) = 3.83 + 0.69 \cdot \ln(x)$	0.80	1.12	48.50	0.0001
Expected no. juvenile spiders as a function of colony size					
2A Rooisand	$\ln(y) = 3.91 + 0.81 \cdot \ln(x)$	0.88	1.19	135.80	0.0001
2B Oupembamewa	$\ln(y) = 4.26 + 0.81 \cdot \ln(x)$	0.72	1.12	41.84	0.0001

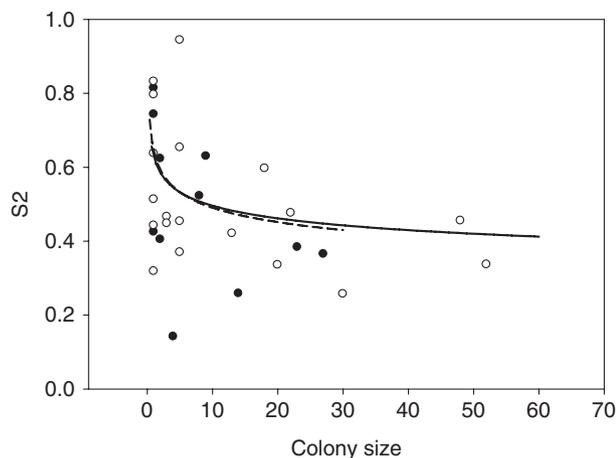


Fig. 3 The probability of survival of hatchlings, from egg to the end of maternal care, S_2 , in Rooisand (●)(—) and Oupembamewa (○)(- -) as a function of colony size. Functions are obtained from equations given in Table 6.

maximum of approximately 4 found at a colony size of 19 females. LRS was calculated for colonies sizes up to 38 females in Rooisand and 25 females in Oupembamewa.

Colony size distribution

The size distribution of 104 colonies was surveyed in Rooisand in February 2003 (just after adult female propagule dispersal) and of 599 colonies in Oupembamewa in December 2004 (prior to dispersal) (Fig. 7). LRS was highest in colonies of intermediate size, but colonies of intermediate size were not the most abundant, rather, small colonies predominated in both populations (Fig. 7). A majority of the small colonies observed in Oupembamewa were daughter colonies established by fission, and these were found in conjunction with and often connected to large colonies. If we excluded such daughter colonies, the size distribution of isolated already established (propagule) colonies followed the prediction from the LRS curve (Fig. 7). Colonies giving rise to daughter colonies by fission were larger than those that had not given rise to daughter colonies and therefore were found in isolation (Pearson: $X^2_{2,313} = 24.324$, $P < 0.0001$), sug-

gesting that dispersal predominantly happens from larger colonies. This result was confirmed as 37% of the large colonies were associated with daughter colonies, compared with 19% of medium sized and only 2% of the small colonies ($n = 596$). The number of daughter colonies associated with a founding nest ranged from 1 to 12. In Oupembamewa, 79% of all observed small colonies were daughter colonies compared with 21% of the medium and 9% of the large colonies.

Discussion

We studied reproductive success and survival as a function of colony size in two populations of the social spider *S. dumicola* to examine whether net fitness increases with colony size, as predicted for social species. This prediction was supported, as we show that LRS increases up to an optimal group size, although the optimum group size and average individual LRS may differ between populations. This is a key result suggesting direct benefits of group living. Additional benefits may arise from potential genetic benefits accrued from high relatedness among group members. Group living affects different fitness components in different ways, hence, a lower average individual reproduction and decreased early offspring survival reveal considerable costs of group living on direct fitness traits. Substantial survival benefits, in particular at the colony level, appear decisive for tipping the balance in favour of group living.

The pattern of opposing forces affecting group living observed in this study are similar to those found in a social theridiid spider, *A. eximius*, where females had a lower probability of reproducing but the offspring had a significantly higher probability of survival with increasing size of the breeding unit (Avilés & Tufiño, 1998). Hence ecological conditions through constraints on colony foundation (see also Henschel, 1993, 1998; Wickler & Seibt, 1993), appear a major selective force in the evolution of permanent sociality in spiders. This is parallel to the social insects, where ecological constraints on colony foundation is considered the driving force in the evolution of social insect societies (Hölldöbler & Wilson, 1977; Herbers, 1986; Bourke & Heinze, 1994). Similarly, ecological constraints via reduced survival of

Table 7 Linear regression of number of spiders on expected number of spiders for colonies collected in Rooisand (equation 1A and 2A) and Oupembamewa (equation 1B and 2B, see also Appendix Fig. A2). Equation 2 was divided by equation 1 to obtain S3. Linear regression of expected number of spiders on colony size for both locations (equation 3A and 3B) relates S3 to colony size (Fig. 4).

		R^2	d.f.	F-ratio	Prob > F
Observed no. spiders related to expected no. spiders					
1A Rooisand, May	$\ln(y) = 0.19 + 0.84 \cdot \ln(x)$	0.88	1.19	133.92	0.0001
2A Rooisand, December	$y = 12.09 + 0.16 \cdot x$	0.61	1.09	13.98	0.0046
1B Oupembamewa, May	$\ln(y) = 1.11 + 0.68 \cdot \ln(x)$	0.71	1.12	30.51	0.0001
2B Oupembamewa, November	$\sqrt{y} = 1.47 + 0.51 \cdot \sqrt{x}$	0.44	1.10	7.71	0.0196
Expected no. spiders in relation to colony size					
3A Rooisand	$y = 90.64 + 26.30 \cdot x$	0.75	1.30	88.55	0.0001
3B Oupembamewa	$\ln(y) = 4.34 + 0.82 \cdot \ln(x)$	0.64	1.24	42.17	0.0001

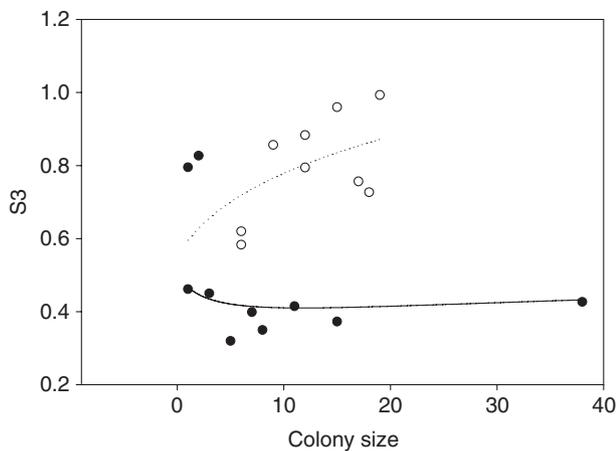


Fig. 4 The probability of survival from juvenile to the sub-adult stage, S3, Rooisand (●) (—) and Oupembamewa (○) (- - -) as a function of colony size. Functions are obtained from equations given in Table 7.

subordinates at dispersal have been used to explain the evolution of cooperative breeding in birds (Stacey & Koenig, 1990), mammals (Solomon & French, 1997) and fish (Heg *et al.*, 2004).

Ecological constraints on survival have strong implications for dispersal. In the social spiders, pre-mating dispersal is probably completely eliminated, leading to reproduction among colony members and subsequently high levels of inbreeding (Avilés, 1997; Lubin & Bilde, 2007). These processes increase relatedness among group members, which accrue inclusive fitness benefits in addition to the direct benefits shown here to be present, thus further promoting cooperation and reducing conflict among group members (West-Eberhard, 1975). The same effects, however, would also increase competition among close kin (Hamilton & May, 1977).

Social spiders show two modes of colony foundation – independent foundation by inseminated females, usually through long distance dispersal (propagule) and colony fission where a colony splits to give rise to two or more smaller daughter colonies (reviewed in Lubin & Bilde, 2007). Although the former strategy is risk prone – our

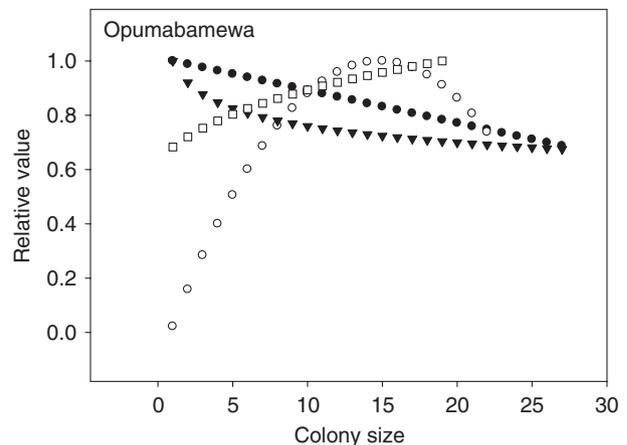
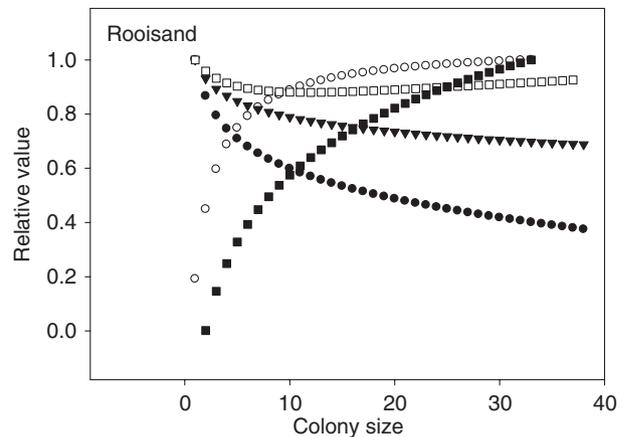


Fig. 5 The relative value of the components of lifetime reproductive success: R1 (●), S1 (○), S2 (▼), S3 (□) S4 (■ only for Rooisand) in (a) Rooisand and (b) Oupembamewa.

study shows that more than 90% of these propagules would go extinct before the next breeding season – it is also rewarding when successful as single females may gain more offspring (e.g. Seibt & Wickler, 1988b; Avilés & Tufiño, 1998). We found colony foundations of both types in our study, and the prevailing dispersal mode seemed to differ between populations: In Rooisand, the

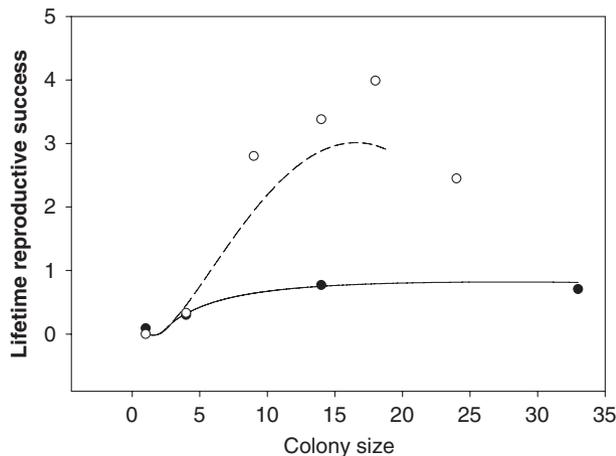


Fig. 6 Lifetime reproductive success (LRS) estimated for colonies of discrete size classes by multiplying the fitness components R1, S1, S2, S3, S4, for Rooisand (●)(—) and for Oupembamewa (○) (- - -); lines are predicted continuous LRS models based on linear regression for the relationship between colony size and number of females.

less productive site, we observed many independent single-female colonies. The LRS estimate here indicated that colonies could barely replace themselves, probably because they occurred at their margin of subsistence on the edge of the hyper-arid Namib Desert. Small propagule colony foundation, as a risk prone strategy, could be rewarding here compared with the low productivity in large colonies. In Oupembamewa, the more productive site, we found a substantial proportion of young colonies that were established through colony fission. Such risk averse strategy should be adaptive at a site where available resources are sufficient to meet or exceed the needs of the average individual, in agreement with risk sensitive foraging theory (e.g. Caraco, 1981; Clark & Mangel, 1986; Uetz & Hodge, 1990; Caraco *et al.*, 1995).

The colony foundation system in social spiders appear parallel to that of facultative polygynous social insects (Hölldöbler & Wilson, 1977; Heinze, 1993). Although in insect colonies foundation by multiple queens may result in intra-colony relatedness lower than in social spider colonies, substantial colony-level survival benefits in both systems appear crucial for group living to evolve (Bourke & Franks, 1995; Avilés & Tufiño, 1998). High productivity or survival of larger groups increases the chance of survival until reproduction and proliferation. These colony-level benefits override individual selection (in this case fecundity selection) within colonies, suggesting a multi-level selection scenario (Maynard Smith, 1976; Wade, 1980; Avilés, 1986, 1993, 1999; Bourke & Franks, 1995; Leigh, 1999; Okasha, 2004). The high level of genetic differentiation among groups because of intra-colony breeding implies that the colonies of social spiders represent relatively isolated population lineages, or

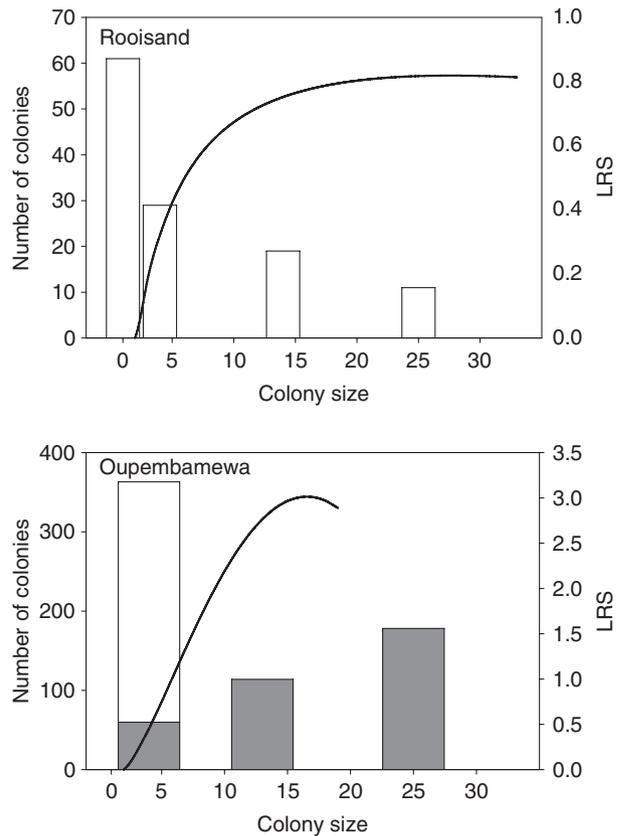


Fig. 7 The size distribution of colonies in the two locations (a) Rooisand and (b) Oupembamewa. In the latter white bars represent all observed colonies (founded by propagules or fission) and grey bars a subset consisting of only propagule colonies. The lifetime reproductive success (LRS) values (Fig. 6) for each location are plotted in the graphs to compare the distribution of colonies with the colony size-dependent LRS curve.

demes, among which selection may act (Smith & Hagen, 1996). Under such conditions, Avilés (1993) showed through computer simulations that inter-colony selection should favour female biased sex ratios because they allow colonies to grow faster and reach sooner the threshold size to either avoid extinction or to reproduce. Similar arguments may apply to the tension between selection for increased reproduction within the colonies and the risk of colony extinction.

Benefits of group living include kin selected cooperative actions that mitigate the costs of group living. Sociality in spiders invariably appears to entail reproductive costs (Seibt & Wickler, 1988b; Avilés & Tufiño, 1998), which likely result from increased intra-colony competition with increasing group size (Ward & Enders, 1985; Rypstra, 1993; Ulbrich & Henschel, 1999; Griffin & West 2002). This would be the case if, for example, prey availability did not increase at a similar rate as group size

(Ward, 1986) and feeding became less efficient when group size increased (Seibt & Wickler, 1988a, Ulbrich *et al.*, 1996; Whitehouse & Lubin, 1999; Amir *et al.*, 2000; Gonzaga & Vasconcellos-Neto, 2001). Competition for food would also explain the reduction in adult female body size with increasing group size found in both our study populations. Reproductive costs may increase conflicts of interest among co-breeding females, but these can be offset if females who fail to reproduce become helpers and contribute to the provisioning of related offspring (West-Eberhard, 1975; Brown & Pimm, 1985; Rypstra, 1993; Keller & Reeve, 1994). Females that provide allomaternal care may mitigate some of the costs of competition while increasing inclusive fitness benefits (West-Eberhard, 1975; Seibt & Wickler, 1987, 1988a,b; Henschel *et al.*, 1995; Lubin & Bilde, 2007). Small groups of *S. dumicola* females in an experimental setup increased the survival and growth of nondescendent young by means of regurgitation feeding and finally by providing their bodies, along with that of the genetic mother, for consumption by the young (Salomon & Lubin, 2007). However, in both study populations survival from egg to the end of the maternal care stage (S2), in colonies that survived to this stage, decreased as colony size increased. These results suggest that although allomaternal care may aid in early offspring survival by preventing the extinction of whole colonies, it may not be sufficient under field conditions of limited prey availability to offset competition for resources leading to increased early-offspring mortality as the breeding group increases.

When analysing the distributions of colony sizes in the field, it was unexpected to find a majority of small colonies rather than finding a high proportion of medium-sized colonies in the size range where LRS was maximized. Ecological and genetic factors perhaps contribute to understanding this phenomenon. Field observations suggest that with age and increasing group size, high intra-colony competition, together with perhaps increased parasitism and nest deterioration, trigger large-scale dispersal events (Crouch & Lubin, 2001). Such dispersal events produce a transient population of relatively small colonies and are often followed by extinction of the source colony. Recurrent inbreeding may also play a role in colony extinction (Riechert & Roeloffs, 1993; Crnokrak & Roff, 1999; Keller & Waller, 2002), increasing the susceptibility to diseases because of lack of genetic variation in resistance genes (Hawley *et al.*, 2005; Calleri *et al.*, 2006; Reid *et al.*, 2007). Although a history of inbreeding would have purged the most damaging deleterious recessive alleles from the gene pool (Barrett & Charlesworth, 1991; Crnokrak & Barrett, 2002; Bilde *et al.*, 2005; Aviles & Bukowski, 2006), the lack of genetic variation increases the risk of a population crash in response to the environmental stress (Bijlsma *et al.*, 1999; Spielman *et al.*, 2004a,b). Such ecological and genetic constraints on the persistence of large groups, together with a transient population of incipient nests, may

explain the preponderance of small colonies observed in the field. Interestingly, when considering only the propagule colonies in Oupembamewa, these were distributed as predicted by the LRS curve with most colonies found in the most productive size range. Such ecological and genetic constraints on colony size and longevity ultimately could explain the lack of diversification in social spider clades, suggesting that sociality in spiders may be an evolutionary dead-end (Agnarsson *et al.* 2006; Johannesen *et al.*, 2007).

To summarize, we show that opposing selective forces act on group living in social spiders: individual reproductive success decreases with increasing group size, whereas survival, in particular at the colony level, increases with colony size and is thus a direct benefit of group living. Hence, group living in social spiders, like the social insects, seem to be selected through ecological constraints on dispersal and propagule colony foundation. The processes underlying survival and growth at different life history stages are still poorly understood. In particular, the negative relationship between offspring survival at early stages of development and colony size is perplexing, given that nonbreeding females participate in brood care and hence should aid offspring survival. Investigations of the role of resource competition on allomaternal care, reproductive asymmetry and helping behaviour may provide better understanding of how colony size affects offspring survival. Another component of the life history that requires further study is the dispersal stage. What are the relative benefits and costs of fission vs. solitary female dispersal, and what are the consequences for colony survival and LRS? The causes of colony mortality must themselves vary with colony size, but these are still poorly understood. Field observations suggest that ecological or life-history constraints may limit group size at least in marginal habitats, and may influence modes of colony foundation.

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References

- Agnarsson, I., Avilés, L., Coddington, J. & Maddison, W. 2006. Sociality in Theridiid spiders: repeated origins of an evolutionary dead end. *Evolution* **60**: 2342–2351.
- Alexander, R.D. 1974. The evolution of social behaviour. *Annu. Rev. Ecol. Syst.* **5**: 325–383.
- Amir, N., Whitehouse, M.E.A. & Lubin, Y. 2000. Food consumption rates and competition in a communally feeding social spider, *Stegodyphus dumicola* (Eresidae). *J. Arachnol.* **28**: 195–200.
- Avilés, L. 1986. Sex-ratio bias and possible group selection in the social spider. *Anelosimus eximius*. *Am. Nat.* **128**: 225–245.
- Avilés, L. 1993. Interdemic selection and the sex ratio: a social spider perspective. *Am. Nat.* **142**: 320–345.
- Avilés, L. 1997. Causes and consequences of cooperation and permanent-sociality in spiders. In: *The Evolution of Social Behavior in Insects and Arachnids* (B. Crespi & J. Choe, eds), pp. 476–498. Cambridge University Press, Cambridge, UK.
- Avilés, L. 1999. Cooperation and non-linear dynamics: An ecological perspective on the evolution of sociality. *Evol. Ecol. Res.* **1**: 459–477.
- Avilés, L. 2000. Nomadic behaviour and colony fission in a cooperative spider: life history evolution at the level of the colony? *Biol. J. Linn. Soc.* **70**: 325–339.
- Aviles, L. & Bukowski, T.C. 2006. Group living and inbreeding depression in a subsocial spider. *Proc. R. Soc. Lond. B.* **273**: 157–163.
- Avilés, L. & Gelsey, G. 1998. Natal dispersal and demography of a subsocial *Anelosimus* species and its implications for the evolution of sociality in spiders. *Can. J. Zool.* **76**: 2137–2147.
- Avilés, L. & Tuffiño, P. 1998. Colony size and individual fitness in the social spider *Anelosimus eximius*. *Am. Nat.* **152**: 403–417.
- Barnard, P. (ed.) 1998. *Biological Diversity in Namibia: A Country Study*. Namibian National Biodiversity Task Force, Windhoek, 332 pp.
- Barrett, S.C.H. & Charlesworth, D. 1991. Effects of a change in the level of inbreeding on the genetic load. *Nature* **352**: 522–524.
- Bijlsma, R., Bundgaard, J. & Van Putten, W.F. 1999. Environmental dependence of inbreeding depression and purging in *Drosophila melanogaster*. *J. Evol. Biol.* **12**: 1125–1137.
- Bilde, T., Lubin, Y., Smith, D., Schneider, J.M. & Maklakov, A.A. 2005. The transition to social inbred mating systems in spiders: role of inbreeding tolerance in a subsocial predecessor. *Evolution* **59**: 160–174.
- Bourke, A.F.G. & Franks, N. 1995. *Social Evolution in Ants*. Princeton University Press, Princeton, NJ, USA.
- Bourke, A.F.G. & Heinze, J. 1994. The ecology of communal breeding – the case of multiple-queen leptothoracine ants. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* **345**: 359–372.
- Brommer, J.E., Gustafsson, L., Pietiäinen, H. & Merila, J. 2004. Single-generation estimates of individual fitness as proxies for long-term genetic contribution. *Am. Nat.* **163**: 505–517.
- Brown, D. 1988. Components of lifetime reproductive success. In: *Reproductive Success* (T. Clutton-Brock, ed.), pp. 439–453. University of Chicago Press, Chicago.
- Brown, C.R. & Brown, M.B. 1996. *Coloniarity in the Cliff Swallow*. University of Chicago Press, Chicago.
- Brown, J.L. & Pimm, S.L. 1985. The origin of helping: the role of variability in reproductive potential. *J. Theor. Biol.* **112**: 465–477.
- Brown, C.R., Stutchbury, B.J. & Walsh, P.D. 1990. Choice of colony size in birds. *Trends Ecol Evol* **5**: 398–403.
- Buskirk, R.E. 1981. Sociality in the Arachnida. In: *Social Insects* (H. R. Hermann, ed.), pp. 281–367. Academic Press, London.
- Calleri, D.V. II, Reid, E.M., Rosengaus, R.B., Vargo, E.L. & Traniello, J.F.A. 2006. Inbreeding and disease resistance in a social insect: effects of heterozygosity on immunocompetence in the termite *Zootermopsis angusticollis*. *Proc. R. Soc. Lond. B* **273**: 2633–2640.
- Caraco, T. 1981. Risk-sensitivity and foraging in group. *Ecology* **62**: 527–531.
- Caraco, T., Uetz, G.W., Gillespie, R.G. & Giraldeau, L.A. 1995. Resource consumption variance within and among individuals – on coloniality in spiders. *Ecology* **76**: 196–205.
- Charlesworth, D. & Charlesworth, B. 1987. Inbreeding depression and its evolutionary consequences. *Annu. Rev. Ecol. Syst.* **18**: 237–268.
- Choe, J.C. & Crespi, B.J. 1997. Explanation and evolution of social systems. In: *The Evolution of Social Behavior in Insects and Arachnids* (J. C. Choe & B. J. Crespi, eds), pp. 499–524. Cambridge University Press, Cambridge, UK.
- Clark, C.W. & Mangel, M. 1986. The evolutionary advantages of group foraging. *Theoret. Pop. Biol.* **30**: 45–75.
- Clutton-Brock, T. 1988. *Reproductive Success*. University of Chicago Press, Chicago.
- Crnokrak, P. & Barrett, S.C.H. 2002. Purging the genetic load: a review of the experimental evidence. *Evolution* **56**: 2347–2358.
- Crnokrak, P. & Roff, D.A. 1999. Inbreeding depression in the wild. *Heredity* **83**: 260–270.
- Crouch, T. & Lubin, Y. 2001. Population stability and extinction in a social spider *Stegodyphus mimosarum* (Araneae: Eresidae). *Biol. J. Linn. Soc.* **72**: 409–417.
- Emlen, S.T. 1984. Cooperative breeding in birds and mammals. In: *Behavioural Ecology* (J. R. Krebs & N. B. Davies, eds), pp. 305–339. Blackwell Scientific, Oxford.
- Gerlach, G. & Bartmann, S. 2002. Reproductive skew, costs, and benefits of cooperative breeding in female wood mice (*Apodemus sylvaticus*). *Behav. Ecol.* **13**: 408–418.
- Gonzaga, M.O. & Vasconcellos-Neto, J. 2001. Female body size, fecundity parameters and foundation of new colonies in *Anelosimus jabaquara* (Araneae, Theridiidae). *Insectes Soc.* **48**: 94–100.
- Griffin, A.S. & West, S.A. 2002. Kin selection: fact and fiction. *Trends Ecol. Evol.* **17**: 15–21.
- Griffin, A.S. & West, S.A. 2003. Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. *Science* **302**: 634–636.
- Hamilton, W.D. & May, R.M. 1977. Dispersal in Stable Habitats. *Nature* **269**: 578–581.
- Hawley, D.M., Sydenstricker, K.V., Kollias, G.V. & Dhondt, A.A. 2005. Genetic diversity predicts pathogen resistance and cell-mediated immunocompetence in house finches. *Biol. Lett.* **1**: 326–329.
- Heg, D., Bachar, Z., Brouwer, L. & Taborsky, M. 2004. Predation risk is an ecological constraint for helper dispersal in a cooperatively breeding cichlid. *Proc. R. Soc. Lond. B* **271**: 2367–2374.
- Heinze, J. 1993. Habitat structure, dispersal strategies and queen number in 2 boreal *Leptothorax* ants. *Oecologia* **96**: 32–39.
- Henschel, J.R. 1993. Is solitary life an alternative for the social spider *Stegodyphus dumicola*? *Namibia Scien. Soc.* **43**: 71–77.
- Henschel, J.R. 1998. Predation on social and solitary individuals of the spider *Stegodyphus dumicola* (Araneae, Eresidae). *J. Arachnol.* **26**: 61–69.

- Henschel, J.R., Lubin, Y.D. & Schneider, J. 1995. Sexual competition in an inbreeding social spider, *Stegodyphus dumicola* (Araneae: Eresidae). *Insectes Soc.* **42**: 419–426.
- Herbers, J.M. 1986. Nest site limitation and facultative polygyny in the ant *Leptothorax longispinosus*. *Behav. Ecol. Sociobiol.* **19**: 115–122.
- Hölldöbler, B. & Wilson, E.O. 1977. Number of queens – important trait in ant evolution. *Naturwissenschaften* **64**: 8–15.
- Johannesen, J., Hennig, A., Dommermuth, B. & Schneider, J.M. 2002. Mitochondrial DNA distributions indicate colony propagation by single matri-lineages in the social spider *Stegodyphus dumicola*. *Biol. J. Linn. Soc.* **76**: 591–600.
- Johannesen, J., Lubin, Y., Smith, D.R., Bilde, T. & Schneider, J.M. 2007. The age and evolution of sociality in *Stegodyphus* spiders: a molecular phylogenetic perspective. *Proc. R. Soc. Lond. B.* **274**: 231–237.
- Keller, L. & Reeve, H.K. 1994. Partitioning of reproduction in animal societies. *Trends Ecol. Evol.* **9**: 98–102.
- Keller, L.F. & Waller, D.M. 2002. Inbreeding effects in wild populations. *Trends Ecol. Evol.* **17**: 230–241.
- Koenig, W.D. 1981. Reproductive success, group-size, and the evolution of cooperative breeding in the Acorn Woodpecker. *Am. Nat.* **117**: 421–433.
- Kraus, O. & Kraus, M. 1988. The genus *Stegodyphus* (Arachnida, Araneae). Sibling species, species groups, and parallel origin of social living. *Verh. Naturwiss. Ver. Hamburg* **30**: 151–254.
- Krause, J. & Ruxton, G.D. 2002. *Living in Groups*. Oxford University Press, Oxford.
- Kullman, E.J. 1972. Evolution of social behavior in spiders (Araneae, Eresidae and Theridiidae). *Am. Zool.* **12**: 419–426.
- Leigh, E.G. 1999. Levels of selection, potential conflicts, and their resolution: the role of the “common good”. In: *Levels of Selection in Evolution* (L. Keller, ed.), pp. 15–30. Princeton University Press, Princeton, NJ, USA.
- Lubin, Y. & Bilde, T. 2007. The evolution of sociality in spiders. *Adv. Study Behav.* **37**, in press.
- Lubin, Y. & Crouch, T. 2003. Trial by fire: Social spider colony demographics in periodically burned grassland. *Afr. J. Zool.* **38**: 145–151.
- Maynard Smith, J. 1976. Group Selection. *Q. Rev. Biol.* **51**: 277–283.
- Maynard Smith, J. & Szathmáry, E. 1995. *The Major Transitions in Evolution*. Oxford University Press, Oxford.
- Mendelsohn, J., Jarvis, A., Roberts, C. & Robertson, T. 2002. *Atlas of Namibia. A Portrait of the Land and its People*. David Philip Publishers, South Africa.
- van Noordwijk, M.A. & van Schaik, C.P. 1999. The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis*. *Primates* **40**: 105–130.
- Okasha, S. 2004. Multilevel selection and the partitioning of covariance: a comparison of three approaches. *Evolution* **58**: 486–494.
- Queller, D.C. 1992. Does population viscosity promote kin selection. *Trends Ecol. Evol.* **7**: 322–324.
- Reeve, H.K. & Keller, L. 1999. Levels of selection: burying the units-of-selection debate, and unearthing the crucial new issues. In: *Levels of Selection in Evolution* (L. Keller, ed.), pp. 3–14. Princeton University Press, Princeton, NJ, USA.
- Reeve, H.K., Westneat, D.F., Noon, W.A., Sherman, P.W. & Aquadro, C.F. 1990. DNA “fingerprinting” reveals high levels of inbreeding in colonies of the eusocial naked mole rat. *Proc. Natl Acad. Sci. USA* **87**: 2496–2500.
- Reid, J.M., Arcese, P., Keller, L.F., Elliott, K.H., Sampson, L. & Hasselquist, D. 2007. Inbreeding effects on immune response in free-living song sparrows (*Melospiza melodia*). *Proc. R. Soc. Lond. B* **274**: 697–706.
- Riechert, S.E. & Roeloffs, R.M. 1993. Evidence for and the consequences of inbreeding in cooperative spiders. In: *The Natural History of Inbreeding and Outbreeding* (N. W. Thornhill, ed.), pp. 283–303. University of Chicago Press, Chicago, IL, USA.
- Rypstra, A.L. 1993. Prey size, social competition, and the development of reproductive division of labor in social spider groups. *Am. Nat.* **142**: 868–880.
- Sachs, J.L., Mueller, U.G., Wilcox, T.P. & Bull, J.J. 2004. The evolution of cooperation. *Q. Rev. Biol.* **79**: 135–160.
- Salomon, M. & Lubin, Y. 2007. Cooperative breeding increases reproductive success in the social spider *Stegodyphus dumicola* (Araneae, Eresidae). *Behav. Ecol. Sociobiol.* DOI 10.1007/s00265-007-0406-2.
- SAS Institute Inc. 1989–2004. JMP version 5.1.2. Copyright © 1989–2004. SAS Institute Inc., Cary, NC, USA.
- Schneider, J.M., Roos, J., Lubin, Y. & Henschel, J. 2001. Dispersal of *Stegodyphus dumicola* (Araneae, Eresidae): they do balloon after all! *J. Arachnol.* **29**: 114–116.
- Seibt, U. & Wickler, W. 1987. Gerontophagy versus cannibalism in the social spiders *Stegodyphus mimosarum* Pavesi and *Stegodyphus dumicola* Pocock. *Anim. Behav.* **35**: 1903–1904.
- Seibt, U. & Wickler, W. 1988a. Bionomics and social structure of ‘Family Spiders’ of the genus *Stegodyphus*, with special reference to the African species *S. dumicola* and *S. mimosarum* (Araneida, Eresidae). *Verh. Naturwiss. Ver. Hamburg* **30**: 255–303.
- Seibt, U. & Wickler, W. 1988b. Why do “family spiders”, *Stegodyphus* (Eresidae), live in colonies? *J. Arachnol.* **16**: 193–198.
- Smith, D.R. & Hagen, R. 1996. Population structure and interdemic selection in the cooperative spider *Anelosimus eximius*. *J. Evol. Biol.* **9**: 589–608.
- Solomon, N.G. & French, J.A. 1997. *Cooperative Breeding in Mammals*. Cambridge University Press, Cambridge.
- Spielman, D., Brook, B.W. & Frankham, R. 2004a. Most species are not driven to extinction before genetic factors impact them. *Proc. Natl Acad. Sci.* **101**: 15261–15264.
- Spielman, D., Brook, B.W., Briscoe, D.A. & Frankham, R. 2004b. Does inbreeding and loss of genetic diversity decrease disease resistance? *Conserv. Genet.* **5**: 439–448.
- Stacey, P.B. & Koenig, W.D. 1990. *Cooperative Breeding in Birds*. Cambridge University Press, Cambridge.
- Uetz, G.W. & Hodge, M.A. 1990. Influence of habitat and prey availability on spatial organization and behaviour of colonial web-building spiders. *Natl Geogr. Res.* **6**: 22–40.
- Ulbrich, K. & Henschel, J.R. 1999. Intraspecific competition in a social spider. *Ecol. Modell.* **115**: 243–251.
- Ulbrich, K., Henschel, J.R., Jeltsch, F. & Wissel, C. 1996. Modelling individual variability in a social spider colony (*Stegodyphus dumicola*: Eresidae) in relation to food abundance and its allocation. *Revue Suisse de Zoologie* Vol.hors série ??: 661–670.
- Vehrenkamp, S.L., Koford, R. & Bowen, B.S. 1988. The effect of breeding-unit size on fitness components in groove-billed Anis. In: *Reproductive Success* (T. H. Clutton-Brock, ed.), pp. 291–304. University of Chicago Press, Chicago.
- Vollrath, F. 1982. Colony foundation in a social spider. *Z. Tierpsychol.* **60**, 313–324.

Wade, M.J. 1980. Kin selection: its components. *Science* **210**: 665–667.
 Ward, P.I. 1986. Prey availability increases less quickly than nest size in the social spider *Stegodyphus mimosarum*. *Behaviour* **97**: 213–225.
 Ward, P.I. & Enders, M.M. 1985. Conflict and cooperation in the group feeding of the social spider *Stegodyphus mimosarum*. *Behavior* **94**: 167–182.
 West, S.A., Griffin, A.S., Gardner, A. & Diggle, S.P. 2006. Social evolution theory for microorganisms. *Nat. Rev. Microbiol.* **4**: 597–607.

West-Eberhard, M.J. 1975. The evolution of social behaviour by kin selection. *Q. Rev. Biol.* **50**: 1–33.
 Whitehouse, M.A.E. & Lubin, Y. 1999. Strategic interference competition by individuals competition in social spider foraging groups. *Anim. Behav.* **58**: 677–688.
 Wickler, W. & Seibt, U. 1993. Pedogenetic sociogenesis via the “Sibling-route” and some consequences for *Stegodyphus* spiders. *Ethology* **95**: 1–18.

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Appendix

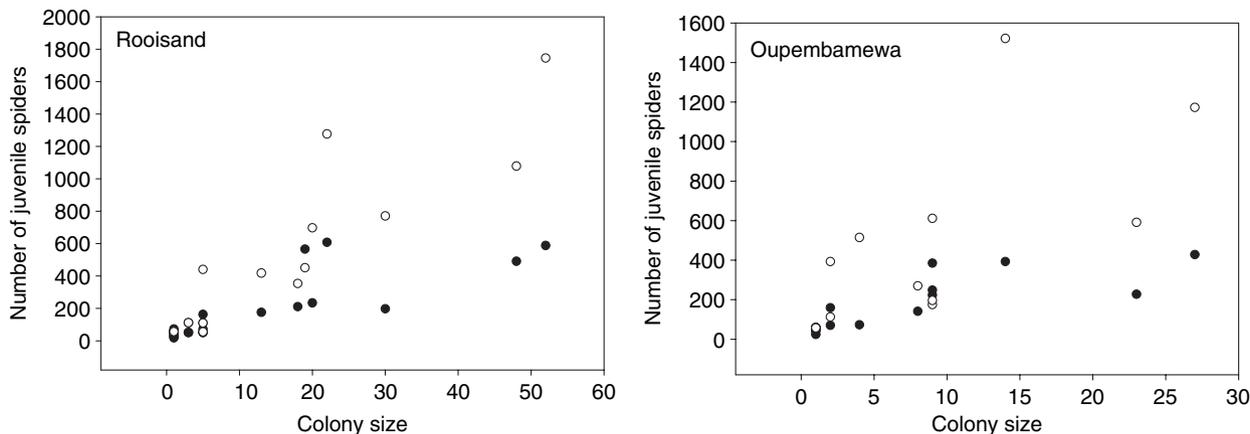


Fig. A1 The relationship between observed number of juvenile spiders in May (●) and the expected number of juveniles in May (○) as a function of colony size. The expected number was calculated from data on reproduction as the product of clutch size and hatching success per female in Rooisand and Oupembamewa.

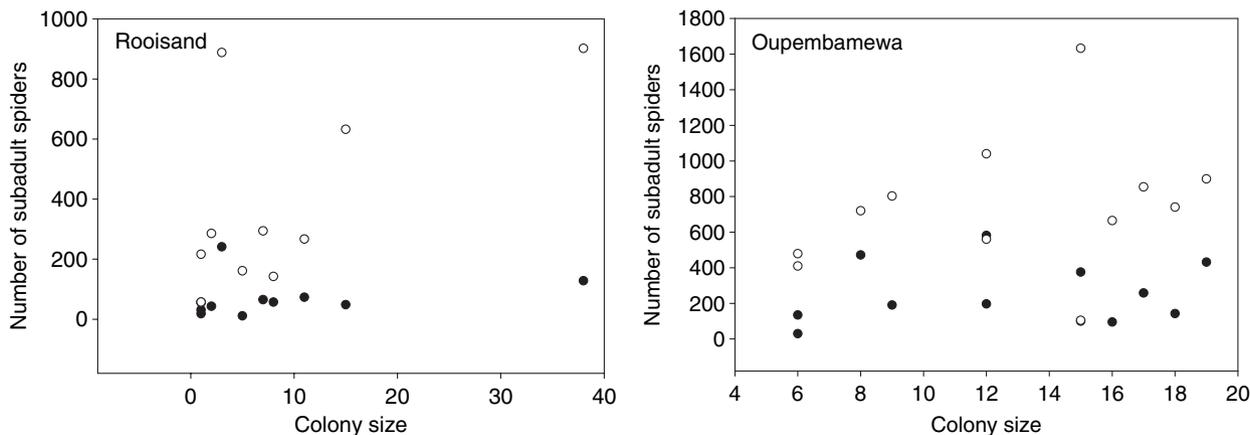


Fig. A2 Data on observed number of subadult spiders in November (●) and the expected number of subadults in November (○) in relation to colony size. The expected number was calculated from data on reproduction as the product of clutch size and hatching success per female in Rooisand and Oupembamewa.