Costs and benefits of joining South American sea lion breeding groups: testing the assumptions of a model of female breeding dispersion

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Abstract: A recent cost–benefit model has been proposed (M.H. Cassini. 1999. Behav. Ecol. 10: 612–616; M.H. Cassini. 2000. Behav. Processes, 51: 93–99) to predict the dispersion of female mammals when breeding resources are distributed in fixed and predictable patches. The benefit of the model is a reduction in male harassment when females join breeding groups, and the cost is an increase in female–female competition for breeding resources. We tested the main assumptions of this model in a breeding colony of South American sea lions (*Otaria flavescens*), a sexually dimorphic, polygynous pinniped. The rate of female–female agonistic interactions increased with the number of females, which suggests that higher levels of female–female competition in denser breeding groups could reduce pup survival, owing to mother–pup separation effects. The rate of male–female interactions per female decreased with the number of females defended by a male, the trend being nonlinear, and males did not modify the frequency of interaction with females according to variations in the size of breeding groups. This evidence supports the advantage of female gregariousness in reducing the reproductive costs of interacting with males. We concluded that avoidance of male disturbance through dilution effects may have played an important role in the evolution of this species' mating system.

Résumé : Un modèle coût-bénéfice récent (Cassini 1999, Behav. Ecol. 10: 612–616; 2000, Behav. Proc. 51: 93–99) a été proposé pour prédire la dispersion des femelles de mammifères lorsque les ressources de la reproduction sont réparties dans des parcelles fixes et prévisibles. Le bénéfice dans le modèle est la réduction du harcèlement par les mâles lorsque les femelles se joignent à des groupes de reproduction et le coût est l'augmentation de la compétition entre les femelles pour les ressources de la reproduction. Nous avons vérifié les présuppositions principales du modèle chez une colonie reproductive d'otaries sud-américaines (*Otaria flavescens*), un pinnipède polygyne à dimorphisme sexuel. Les interactions agonistiques entre femelles augmentent avec le nombre de femelles, ce qui fait croire que les niveaux plus élevés de compétition entre les femelles dans les groupes de reproduction plus denses pourraient réduire la survie des petits à cause des séparations des petits de leur mère. Les interactions mâles–femelles par femelle diminuent avec le nombre de femelles contrôlées par un même mâle selon une tendance non linéaire; les mâles ne changent pas la fréquence de leurs interactions avec les femelles selon les variations dans la taille du groupe de reproduction. Ces données confirment l'avantage du comportement grégaire chez les femelles pour réduire les coûts reproductifs des interactions avec les mâles. Nous concluons que, chez cette espèce, l'évitement des perturbations causées par les mâles au moyen d'effets de dilution a joué un rôle pertinent dans l'évolution de son système de reproduction.

[Traduit par la Rédaction]

Introduction

Because most mammalian mating systems ultimately depend on female dispersion (Davies 1991), the study of habitat selection by breeding females can help in understanding the ecology of mating systems. Cassini (2000) developed a cost–benefit model of breeding dispersion of females that is based on the concept of "ideal free" distribution (Fretwell and Lucas 1970; Tregenza 1995; Sutherland 1996). This model describes population dispersion as the result of individual decisions on habitat selection.

Cassini's (2000) model is applicable to any mammalian species whose resources are distributed in fixed and predictable patches. The intrinsic quality of the patches depends on the ecology of the species under consideration and is related to the resources defended by territorial males in order to gain access to females. The currency of the model is the probability of offspring survival, the cost of aggregating in groups is an increase in female–female competition for resources required for breeding (e.g., grazing areas for ungulates, Carranza and Valencia 1999; tide pools to reduce thermoregulatory stress for pinnipeds, Vilá and Cassini 1990), and the benefit is a reduction in male harassment. The importance of the avoidance of male disturbance as a determinant of breeding aggregations of female mammals has been studied mainly in ungulate leks (Clutton-Brock et al. 1992, 1993; Stillman et al. 1993; Nefdt 1995; Carranza

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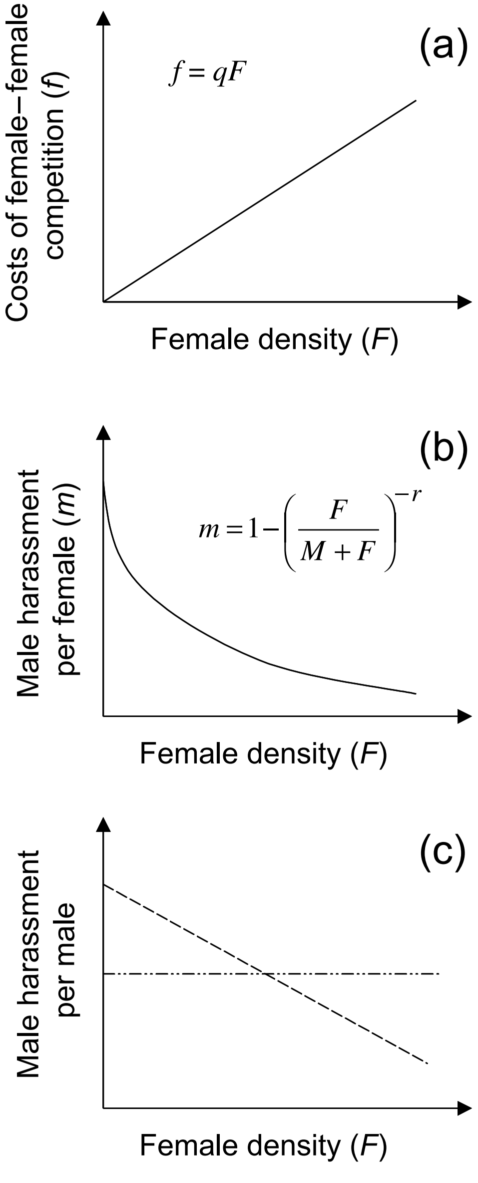
and Valencia 1999) and pinniped colonies (Trillmich and Trillmich 1984; Le Boeuf and Mesnick 1991; Boness et al. 1995; Cassini 1999; Galimberti et al. 2000). The model predicts that male harassment forces females to form denser aggregations than expected according to the distribution of resources (Cassini 2000). Within dense aggregations, a reduction in male harassment compensates for the increase in female competition.

The model makes three main assumptions that have received relatively little empirical consideration. The first assumption is that female interference would increase with the size of breeding groups or units (e.g., males that defend a group of females or a territory with females), and that this increase would be linear (Fig. 1*a*; Cassini 2000). The rate of aggressive interactions between breeding females can be used as an indicator of female interference (Cassini 2001). Agonistic interactions between adult females reduce the time spent with pups (e.g., nursing) and increase the chances of mother–pup separation (Le Boeuf and Campagna 1994), reducing pup survival as a result (Christenson and Le Boeuf 1978; Bowen 1991; Harcourt 1992). Therefore, we assume that in female groups with high levels of aggression, female reproductive success is lower than in groups with low rates of aggression. Cassini (1999) further discusses how differences in female aggressive behavior may affect the fitness of different pinniped families.

The other two assumptions are related to male harassment, which can be assessed from the perspective of females or males. The second assumption is that if only the holder of a breeding unit harasses females, male harassment would decrease in larger breeding units, considering the costs per breeding female (Fig. 1*b*; Cassini 2000). This implies that each female would interact less with resident males which monopolize more females than with males having fewer females, owing to a "dilution" effect (Hamilton 1971; Trillmich and Trillmich 1984; Boness et al. 1995; Galimberti et al. 2000). A solitary female will decrease her chance of being harassed by half if she approaches a second female. As more females join together, the probability of male disturbance decreases, although the rate of benefit decreases, since the reduction in male–female interactions per female is nonlinear (Fig. 1*b*). Finally, the third assumption, which follows from the previous one, is that the rate of male–female interactions per resident male would not vary or would decrease with the number of females being defended (Fig. 1*c*; Cassini 2000). The reason is that if males increased their harassment rate in proportion to the number of females in their breeding units, the dilution effect would not occur.

In this paper, we test these three assumptions using the South American sea lion (*Otaria flavescens*) as the model species. This sexually dimorphic and polygynous pinniped forms breeding colonies where males defend territories and females (Campagna and Le Boeuf 1988*a*, 1988*b*). Female–female aggression is associated with the protection of pups within the colony (Le Boeuf and Campagna 1994; Cassini 2001). Harassment of females is initiated by males with and without females. The most obvious forms of harassment are caused by satellite males without females that try to obtain mates through two strategies: (1) retaining females that arrive from the sea and try to get into the breeding group, and (2) initiating group raids into the breeding area to seize females (Campagna et al. 1988*a*). The detrimental effect of these types of male harassment on female reproductive success can be dramatic, as males may injure females (Campagna et al. 1988*a*; Vilá and Cassini 1990), wound or kill pups (Campagna et al. 1988*b*), or produce massive movements of females, which may become separated from their pups (Campagna et al. 1988*b*; Vilá and Cassini 1990; Campagna et al. 1992). Another type of male harassment, which has received less consideration, is caused by males with females. Resident males with stable breeding units and satellite males that have recently obtained a female show diverse

Fig. 1. The main assumption of Cassini's (2000) model of the breeding distribution of female pinnipeds. (*a*) Costs of female–female competition, which increase linearly with the density of females in breeding groups. (*b*) Costs of male harassment from the females' point of view, which decrease nonlinearly as female density increases. (*c*) Male harassment from the males' perspective, which is implicitly assumed to be constant or to decrease as female density increases. *M*, male density; *q*, female interference coefficient; *r*, male interference coefficient.



forms of interaction with females: nose touches, olfactory inspections of female genitals, mounts, aggressive displays, fights, and physical blocking of female movements when females search for their pups or run away. This paper reports male harassment within breeding units, which can affect female reproductive success, mainly by reducing mothers' care of pups and eventually increasing mother–pup separations (e.g., Le Boeuf and Campagna 1994).

Methods

Breeding colonies of South American sea lions are distributed from the Atlantic coast of southern Brazil, Uruguay, and Argentina to the Pacific coast of Chile and Peru. This study was carried out at Punta Norte on the coast of Península Valdés, Argentina (42°04′S, 63°47′W), during the 1994–1995 breeding season, totaling 39 days of observation during December–January. The assumptions of Cassini's (2000) model were tested during the period when most breeding decisions were made (joining breeding groups, birth, copulation, and the first part of the lactation period) to minimize temporal variations in the levels of male harassment.

During our study, we recorded a total of 444 females, 129 adult males, 79 subadult males, and 431 pups at Punta Norte. To reduce thermoregulatory stress, most breeding individuals aggregated just above the high-tide line or central breeding area, where the substrate remained wet. The colony substrate was a uniform pebble beach without tide pools or vegetation (Campagna 1985; Campagna and Le Boeuf 1988*a*, 1988*b*). Because of the homogeneity of the colony substrate, males increased their mating success by sequestering and keeping females within breeding units in the central breeding area instead of defending rigid territories (Campagna et al. 1992). Breeding success was substantially lower outside of the central breeding area (Campagna et al. 1992). Based on all focal observations (n = 257), the mean size of breeding units was 2.94 individuals (SD = 2.75 individuals). Overall, during our study the behavior of breeding individuals was similar to previous descriptions of the same colony (e.g., Campagna 1985; Campagna and Le Boeuf 1988*a*, 1988*b*; Werner and Campagna 1995; Fernández-Juricic et al. 1999).

The study subjects were 24 females and 20 males, which were marked with paint pellets (Campagna and Le Boeuf 1988*a*). Marking took place mainly during the first week of this study, before the density of the colony reached its peak, which allowed us to mark individuals at the center as well as at the periphery of the colony. Four of the 20 males were identified on the basis of natural marks (e.g., little hair on the head and neck). More individuals than the 44 study subjects were marked during the breeding season, but we only considered those that could be recognized accurately throughout our sampling period. Moreover, we studied only breeding females that occupied a position in the colony, not wandering females. The distribution of marked females in relation to marked males was very dynamic because animals redistributed themselves after marking as a result of the increase in the density of individuals, fights between males, group raids, feeding trips by females, etc. The maximum number of marked females per marked male was 2, which happened 7 times during the breeding season. Marked individuals received an evenly spread sampling effort during the study so that individuals had similar numbers of focal observations per week. On average, each individual was sampled 7.07 times (SD = 3.04 times). Each day, we determined the number and location of marked individuals available in the colony, randomly chose 5–7, and conducted 30-min focal observations (Altmann 1974) on them. On subsequent days, we followed similar procedures but tried to keep the numbers of focal observations per individual similar at the end of the sampling period.

During focal observations we recorded the numbers of female–female and male–female interactions. In a recent study (E. Fernández-Juricic and M.H. Cassini, unpublished data) we found that female agonistic interactions were generally limited to females within a breeding group defended by an adult male, with little interaction between breeding groups. Therefore, we tested the predictions of Cassini's (1999) model considering the breeding group as the unit of male–female and female–female interactions.

Female–female agonistic interactions comprised three behavioral events (Campagna and Le Boeuf 1988*a*; Vilá and Cassini 1990; Fernández-Juricic et al. 1999): open-mouth display (the female's head was oriented towards her opponent, with the lower canines visible and the vibrissae pulled back), grunt (a low-intensity, low-frequency call directed towards female opponents), and fight (a female bit her opponent on the head or neck). All these types of agonistic interactions directed towards a female modified her behavior because she responded with another agonistic interaction or retreated to another sector of the breeding unit (see also Fernández-Juricic et al. 1999; Cassini 2001). Male–female interactions included physical blocking by males of the movements of sexually receptive females when they tried to run away, nose touches directed to particular females, olfactory inspection of female genitals, mounts, and fights. We did not include male growl vocalizations as a male–female interaction because it was difficult to determine accurately the recipient of these calls. We also recorded the number of females defended per male. Females were considered to be associated with a male when they were less than two female body lengths from the focal animal, a criterion usually used in this species to study breeding strategies of both males and females (e.g., Campagna and Le Boeuf 1988*a*; Fernández-Juricic et al. 2001). A male was considered a neighbor when he had defended a position adjacent to a study male for at least 3 days (Campagna and Le Boeuf 1988*a*).

For most statistical analyses, we calculated the average number of interactions (female–female or male–female) within 30 min per marked individual throughout the breeding period. Hence, our sample size equaled the total number of marked females and males.

To calculate the rate of male–female interactions from the perspective of females and males (Figs. 1*b*–1*c*), we considered focal observations of only females and males, respectively. Focal observations of females would indicate the rate of interaction of a focal female (per-capita interaction per female) with the resident male. We only considered the resident male because when group raids took place it was not possible to determine precisely the rate at which focal females interacted with other males, owing to the large num-

Table 1. Relationship between the rate of female–female agonistic interactions in South American sea lions (*Otaria flavescens*) and the number of females defended by a male.

	Regression analysis			Shapiro–Wilk test	
	R^2	$F_{[1,22]}$	p	W	p
Linear model	0.236	6.805	0.0160	0.924	0.0702
Logarithmic model	0.232	6.639	0.0172	0.915	0.0459
Quadratic model	0.235	6.803	0.0161	0.932	0.1057
Exponential model	0.193	5.263	0.0317	0.970	0.6680

Note: Results from linear regressions testing the fit of linear and nonlinear (logarithmic, quadratic, exponential) models to the observed data. Also shown are the results of a Shapiro–Wilk test on the normality of the residuals; a significant result indicates deviation from normality.

ber of individuals interacting simultaneously. Focal observations of males would indicate the rate of interaction of a focal male with the different females in his group (per-capita interaction per male).

We determined whether the patterns of the following relationships were linear or nonlinear: rate of female–female agonistic interactions and number of females defended by a male (Fig. 1*a*), and rate of male–female interactions per female and number of females defended by a male (Fig. 1*b*). We followed Kennedy's (1998) approach whereby nonlinear models are transformed to fit the basic structure of the linear model: $y = a + bx$, where a and b are constants and y and x are the dependent and independent variables, respectively. Three nonlinear models were considered: logarithmic ($y = a + b \log x$), quadratic ($y = a + bx^2$), and exponential ($y = a + \exp(bx)$. With linear regressions, we then compared the fit of the non-transformed linear model versus the transformed nonlinear models through analysis of the significance of the relationship, R^2 values, and the normality of residuals. Significant models, with normal residuals and the highest R^2 values, were considered to be the best fits to the observed data.

Finally, we employed a linear regression to analyze the influence of the number of females defended by a male on the rate of male–female interactions per male (Fig. 1*c*). We pooled all the focal observations made on only one occasion in order to contrast the rates of male–female interactions (from the males' perspective) when males defended one or more than one female (one-way ANOVA test). We also report the power of nonsignificant relationships (G-Power 2.0).

Results

The rate of female–female agonistic interactions increased with the number of females defended by a male (Fig. 2). The linear analysis without transformation of the data showed a significant effect, with the residuals of the regression following a normal distribution (Table 1). The three nonlinear models tested did not improve the linear model. The logarithmic model showed a similar R^2 value to the linear model, but the residuals were not normally distributed (Table 1). The R^2 value of the exponential model was lower than the values of the other three models (Table 1). The quadratic model was the only one whose fit was similar to the linear model (but not better) and whose residuals followed a normal distribution (Table 1). Since the fits of the linear and quadratic models were so similar, we included both terms in a multiple regression analysis with forward-selection procedures to identify which would fit the data when considered concurrently. The model selected only the linear term ($R^2 = 0.236$, $F_{[1,22]} = 6.805$, $p = 0.0160$), and did not include the quadratic term, owing to a lack of significance ($R^2 < 0.01$, $F_{[1,21]} = 0.07$, $p = 0.791$). This result cannot be considered conclusive, given the similarity in the fit of the linear and quadratic models, but it suggests that the linear model was a better predictor of the observed variability.

Fig. 2. Relationship between the rate of female–female agonistic interactions and the number of females defended by a male. Dotted lines show the 95% confidence bands.

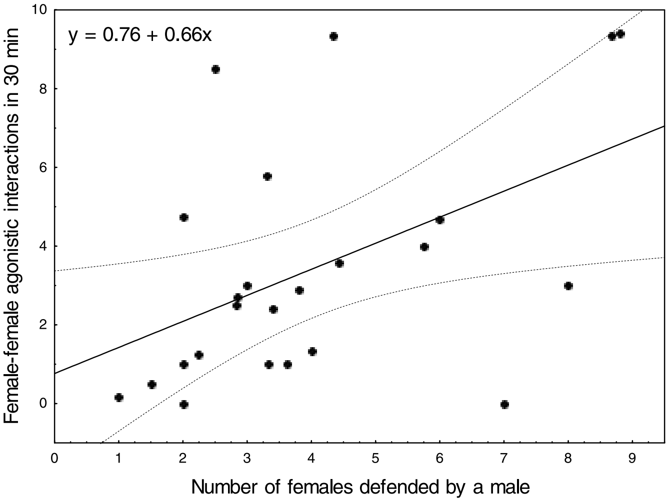
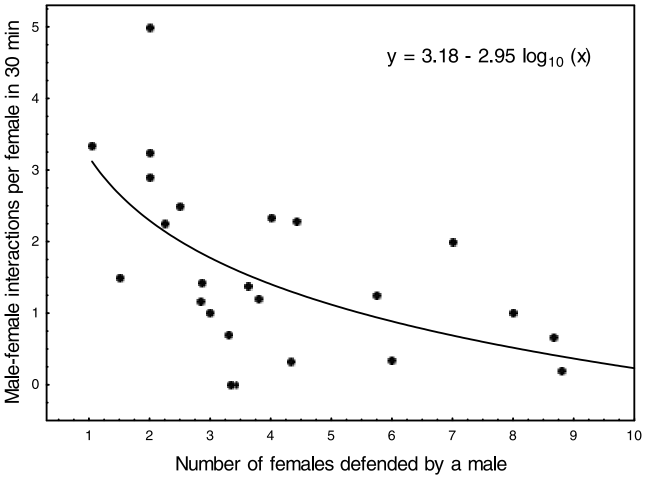


Fig. 3. Relationship between the rate of male–female interactions per female and the number of females defended by a male.



The rate of male–female interactions per female decreased with the number of females defended by a male (Fig. 3). The model that best fitted the data was the logarithmic one, the distribution of residuals being normal (Table 2). However, a closer look at Fig. 3 shows that one point at the top left corner of the graph may have affected this relationship. This point was identified as the main outlier through Cook's dis-

Table 2. Relationship between the rate of male–female agonistic interactions per female and the number of females defended by a male.

	Regression analysis			Shapiro–Wilk test	
	R^2	F	P	W	P
Original data (df = 1,22)					
Linear model	0.249	7.305	0.0129	0.962	0.4841
Logarithmic model	0.334	11.014	<0.001	0.968	0.6093
Quadratic model	0.179	4.786	0.0396	0.962	0.4943
Exponential model	0.225	6.373	0.0193	0.958	0.4026
Without outlier (df = 1,21)					
Linear model	0.238	6.545	0.0183	0.963	0.5451
Logarithmic model	0.328	10.286	0.0042	0.969	0.6986
Quadratic model	0.172	4.356	0.0492	0.969	0.6792
Exponential model	0.195	5.081	0.0349	0.942	0.2170

Note: Values are from linear regressions testing the fit of linear and nonlinear (logarithmic, quadratic, exponential) models to the observed data. Also shown are the results of a Shapiro–Wilk test on the normality of the residuals; a significant result indicates deviation from normality. Two datasets were analyzed: the original data (including all females sampled) and without the outlier (i.e., excluding a female whose mean interaction rate could have biased the shape of the relationship; see the text).

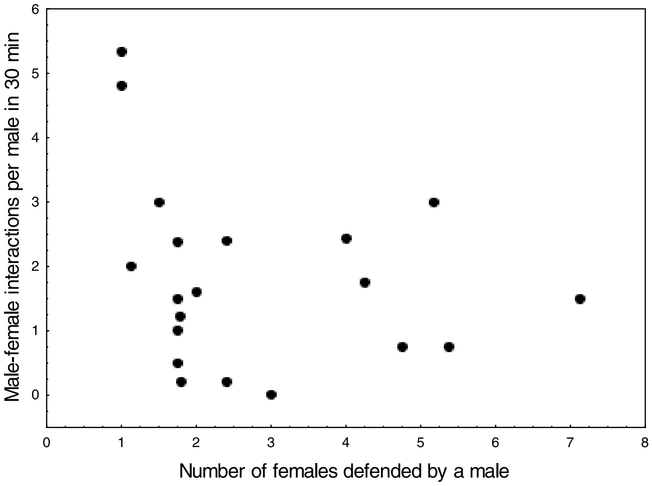
tance analysis, which is an indicator of whether or not an observation is an outlier with respect to the values of the independent variable. We carried out the analyses again without this outlier and the results were similar (Table 2): the logarithmic model explained a greater proportion of the variability. This suggests that the decrease in the rate of male–female interactions per female was a decelerating function of the number of females defended by a male.

The rate of male–female interactions per male showed no significant relationship with the number of females defended by a male (lineal regression analysis, R^2 = 0.06, $F_{[1,18]}$ = 1.23, p = 0.282, power = 0.22; Fig. 4). However, Fig. 4 shows a slight increase in the number of interactions when males defended one female on the average. We then pooled all focal observations and compared males' behavior towards females when they were defending one and more than one female. The rate of male–female interactions did not differ significantly between the two conditions (ANOVA, $F_{[1,106]}$ = 0.06, p = 0.812, power = 0.11; one female, 1.80 ± 0.41; more than one female, 1.93 ± 0.37). Therefore, the rate of male–female interactions per male remained relatively constant despite variations in the number of females. However, this result should be regarded with caution because of the low power of the analyses.

Discussion

The three main assumptions of Cassini's (2000) model were tested in a breeding colony of South American sea lions, and the findings were as follows: (1) the rate of female–female agonistic interactions increased with the number of females, (2) the rate of male–female interactions per female decreased with the number of females defended by a male, with a trend towards nonlinearity, and (3) the rate of male–female interactions per male did not vary with the number of females defended by a male.

Fig. 4. Relationship between the rate of male–female interactions per male and the number of females defended by a male.



According to this model, the main factor forcing females to aggregate is the risk caused by male disturbance. A resident male disturbs his females when they try to avoid mounting and copulation attempts or try to stray because of disturbances or high temperatures (Campagna and Le Boeuf 1988*a*; Vilá and Cassini 1990), which could affect female reproductive success. The rationale is that as female group size increases, the proportion of females per male increases and the effect of male disturbance will be diluted (Hamilton 1971; Boness et al. 1995; Cassini 2000; Galimberti et al. 2000). This dilution effect occurs because male–male sexual competition limits the number of males defending female aggregations within a breeding colony. Such a dilution effect would not be apparent without male–male competition, because the number of males, along with the levels of male harassment, would increase in proportion to the number of females.

Campagna et al. (1992) showed that when female density increases within breeding units, female reproductive success also increases. They compared pup mortality rates at two levels of female density (one versus more than one female) and under two social conditions (isolated breeding units versus colonies). In isolated breeding units with one female, pup mortality was as high as 60%, while in breeding units with more than one female, there was no pup mortality. In breeding units within the colony, they compared mortality of pups born early and at the peak of the breeding season. Between the two periods the number of males remained constant, but there was a substantial increase in the size of breeding units because of female arrivals. Pup mortality was 32% when breeding units were small early in the season and less than 1% at the peak of the season. The main causes of pup mortality in small breeding units were starvation and infanticide. Differences in pup mortality between breeding units of different sizes cannot be explained by higher rates of raiding, because large breeding units are more exposed to male raids than small ones (Campagna et al. 1988*a*). However, males defending small breeding units could be less efficient when protecting females from harassment by satellite males. Another explanation of the mechanism underlying the phenomenon described by Campagna et al. (1992) is provided by our study. We have shown that males holding small breeding units interacted more frequently with their females. This male harassment would reduce mothers' protection of pups and increase the probability of mother–pup separation, ultimately increasing the risk of starvation and infanticide.

Large breeding units provide an environment with a lower chance of male–female interactions (Fig. 3). However, large groups also imply higher levels of competition between females (Fig. 2). Aggressiveness of female South American sea lions is usually associated with protecting pups and thus increasing their likelihood of survival (Cassini 1985; Vilá and Cassini 1990). An increase in the level of female aggressiveness in large breeding units in relation to small ones has also been reported for other pinniped species (Christenson and Le Boeuf 1978; Harcourt 1992; Cassini 2001).

Our results cannot be used to test the equilibrium predictions of Cassini's (2000) model, i.e., determine the optimum breeding-group size at which the benefits of avoiding male harassment equal the costs of female competition. They only indicate that breeding units of South American sea lions meet the assumptions of Cassini's (2000) model, and that variations in the degree of male harassment and female interference could cause variations in fitness (e.g., female and pup survival). The reason is that explicit conversion of the costs of male–female and female–female behavioral interactions into fitness costs would be necessary. Previous studies have established these links in different pinniped families (e.g., Cassini 1999, 2000). In future studies to test the equilibrium predictions of Cassini (2000), an alternative approach would be to use the same currency to estimate the costs of male harassment and female interference, so that receiving aggression from another female or from a male would entail equivalent costs for a breeding female. The best currency would be the probability of pup mortality.

Our study, however, suggests interesting theoretical considerations that deserve further testing in the context of the evolution of mating systems (see also Clutton-Brock et al. 1993; Carbone and Taborsky 1996; Thirgood et al. 1999). Mate choice by female social pinnipeds has been traditionally explained as a form of "good-gene" selection, and colonies have been interpreted as arenas from which to select mates (e.g., Cox and Le Boeuf 1977). An alternative approach is to consider the evolution of mate choice in the social context of avoiding male disturbance in such a way that females could develop a preference for males with characteristics which protect them from disturbance by other males. Initially, females could form groups by means of a "selfish-herd" mechanism (Hamilton 1971), i.e., staying near other females, thereby diluting the effect of male disturbance (Bartholomew 1970; Trillmich and Trillmich 1984). Cassini (1999) proposes that a positive feedback loop could be created, with females joining larger and denser groups to avoid male harassment, intensifying male intrasexual selection and increasing the proportion of marginal males that interact with females, promoting, in the end, female gregariousness. This context of social evolution should facilitate the emergence of a preference for males with traits that protect females from male harassment: mainly males that prevent disturbance by other males, and males that themselves show a low propensity to disturb females. The fact that female South American sea lions interacted less with males in large breeding units makes this species an interesting model to use for testing whether females select males that show a low propensity for disturbance.

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