

Parental Effort and Reproductive Skew in Coalitions of Brood Rearing Female Common Eiders

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ABSTRACT: Members of breeding groups face conflicts over parental effort when balancing antipredatory vigilance and feeding. Empirical evidence has shown disparate responses to manipulations of parental effort. We develop a model in which we determine the evolutionarily stable effort of partners given their body conditions, allowing the benefits of shared care to be unevenly divided, and we test this model's predictions with data on common eiders (*Somateria mollissima*). Eiders show uniparental female care; females may share brood rearing, or they may tend alone, and their body condition at hatching of the young shows large environmentally induced variation. The model predicts that parental effort (vigilance) in a coalition is lower than when tending alone, controlling for parental condition; this prediction is supported by the data. The parental effort in a coalition should be positively correlated with body condition, and this prediction is also supported. Finally, parental effort should increase when partner condition decreases and vice versa; this prediction is partially supported. The Nash bargaining game may provide promising avenues by which to determine the precise settlement of reproductive skew and effort between coalition partners in the future.

Keywords: parental effort, parental care game, body condition, vigilance, *Somateria mollissima*, Nash bargaining game.

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How hard a parent should work is a central question in behavioral ecology (Hails and Bryant 1979; Roff 1992). This level of effort depends on the trade-off between the benefits of current investment for brood fitness and the costs of that investment for future survival and reproduction (Williams 1966; Stearns 1992). In social breeding groups, however, the level of effort of one parent cannot be determined by simply optimizing this trade-off but depends also on the amount invested by the cooperating partner(s) (Houston and Davies 1985; Winkler 1987). A number of empirical studies have shown that a parent responds directly to the effort of its partner(s) (reviewed in Sanz et al. 2000; Smiseth and Moore 2004).

Each member of a social breeding group has to balance the proportion of time it spends scanning for predators with the time it spends feeding, each preferring to feed as much as possible and therefore preferring the others to be vigilant. This is a classic example of a conflict between cooperating individuals (Pulliam et al. 1982; Lima 1987; McNamara and Houston 1992), which in many dioecious species takes the form of a sexual conflict over parental effort (Houston and Davies 1985; Houston et al. 2005). However, males and females differ in various ways, so that their cost and benefit functions of parental effort may be different (e.g., Velando and Alonso-Alvarez 2003). As a consequence of these inherent sexual differences, male and female breeders do not use the same decision rules over parental investment, and this will tend to obscure interpretations about the parental effort of cooperating male and female partners.

Most standard two-player game theory models, including the renowned Houston-Davies model of parental care (Houston and Davies 1985), assume that players in a given role (e.g., males and females) are identical. This assumption is unrealistic, since individuals will differ in aspects of quality that influence the costs and benefits of performing actions such as parental care (McNamara et al. 1999). One attribute linked to an animal's quality as a parent is the amount of body reserves at its disposal. Per-

manent monitoring of own body condition is expected to be essential in reproductive decisions (Drent and Daan 1980), and animals adjust their level of parental investment according to their body reserves, so as not to jeopardize their survival and future breeding success (Chastel et al. 1995; Erikstad et al. 1997; Kilpi et al. 2001). Many animals regularly lose mass during breeding, and parents with high reserves can provide better care than parents with low reserves (Tveraa et al. 1998; Barta et al. 2002; Öst et al. 2003a). Especially in long-lived species, current reproductive investment is more likely to be regulated by the impact of reproductive effort on the future reproduction of the parents, and adults should be restrictive in increasing their effort (e.g., Clark and Ydenberg 1990; Velando and Alonso-Alvarez 2003). There is also some evidence from long-lived seabirds suggesting that parents are able to exchange information about their current body condition (Tveraa et al. 1997), which in turn may affect the parental effort levels of the sexes.

The standard method to test the response of one parent's parental effort to changes in the effort of the other is to increase or reduce the effort of the partner through experimental manipulations (e.g., Monaghan and Nager 1997; Sanz et al. 2000; Velando and Alonso-Alvarez 2003). This experimental evidence has shown a range of responses to a reduction in a partner's parental care, from a negative or no response through incomplete compensation to complete compensation. The large spread of these results is perhaps not altogether surprising, considering the ubiquitous sexual differences in parental investment patterns. The parental efforts of group members in socially breeding groups may also be sensitive to other confounding variables, such as kinship among participating individuals (Hartley and Davies 1994; Hatchwell 1999). Experimental manipulations also do not manipulate the reproductive effort directly (Tammaru and Hörak 1999), and the compensatory parental effort response of one parent resulting from manipulation of the other parent may be the result of the experimental treatment itself, instead of being the desired consequence of a reduction in reproductive effort per se. For example, testosterone implants and weighting and feather cutting may change the perception of mate attractiveness (Paredes et al. 2005; Hinde 2006). So far, studies analyzing variation in parental effort in social breeding systems characterized by large natural variation in both parental effort and parental quality are remarkably few.

Common eider ducks (*Somateria mollissima*) are long-lived seabirds characterized by uniparental female care; females may rear broods alone, or they may pool their broods and share brood rearing, usually in coalitions of two to four females (Bustnes and Erikstad 1991; Kilpi et al. 2001; Öst et al. 2003b). Large natural variation in female

body condition at hatching of the young exists because incubation is accomplished without feeding (e.g., Parker and Holm 1990). This variation is largely environmentally induced and thus unpredictable, depending as it does on the severity of weather during incubation (Kilpi and Lindström 1997; this study). Poor body condition is associated with low success in lone reproduction (Bustnes and Erikstad 1991; Kilpi et al. 2001; Öst et al. 2003a). Parental effort of females mainly takes the form of close guarding of the brood and shows large interindividual variation (Öst et al. 2002). The recovery of body condition during brood rearing is difficult, because habitats with good feeding for ducklings do not offer good feeding opportunities for hens (Öst and Kilpi 1999). Condition therefore has a strong effect on the choice of brood rearing tactics (lone vs. joint brood tending) as well as on the choice of suitable coalition partners (Öst et al. 2003b).

In their partner choice model, Öst et al. (2003b) assumed that brood rearing ability is enhanced in coalitions, but because the favorable central positions for ducklings in the joint brood are necessarily limited, the hens must share the heightened benefits. The allocation need not be equal: low-condition females have poor prospects as lone tenders, so potential partners need not concede much of the joint benefit to attract them to the coalition. Öst et al. (2003b) successfully predicted that hens with increasingly good condition formed coalitions only with hens in increasingly poorer condition.

Condition appears also to affect the effort that hens are able to devote to brood rearing (Öst et al. 2003a), and in this study we investigate this aspect of common eider breeding. We develop a model in which we determine the evolutionarily stable efforts of partners given their body conditions, allowing the benefits of joint brood care to be unevenly divided among the females. We test this model's predictions with data obtained during several field seasons. The common eider is an ideal study object for observing the division of parental effort between cotending parents because the sexual differences that complicate predictions about parental effort in most studies are absent. Furthermore, because females form nonkin brood rearing coalitions (Öst et al. 2005), variation in parental effort is not confounded by relatedness among group members.

Partner Effort Model

The partner effort model developed here is derived directly from the parental effort model of McNamara et al. (2003). Partners are indexed by the subscript i . Each partner devotes effort u_i ($0 \leq u_i \leq 1$) to rearing the joint brood, which yields reproductive success $B(u)$, where $u = u_1 + u_2$. We assume that there are diminishing returns on extra effort (i.e., $B'(u) > 0$ and $B''(u) < 0$).

McNamara et al.'s (2003) model considers two parents, each of whom necessarily (barring extrapair paternity) has an equal stake in the brood. In the partner effort game this is not so. Partners may have different numbers of ducklings, and the ducklings may occupy positions of different survival value in the joint brood. We compress all of this biology into a simple "skew" parameter that divides the total reproductive success between the partners, with proportion s going to partner 1 and $1 - s$ to partner 2. Each female pays a fitness cost related to her own effort, $K_i(u_i)$, where K_i depends on condition such that a given level of effort is more costly with lower condition. We assume that costs accelerate with effort (i.e., $K'_i(u_i) > 0$ and $K''_i(u_i) > 0$). For given s , u_1 , and u_2 , the fitness of partner 1 in a coalition is

$$sB(u_1 + u_2) - K_1(u_1), \quad (1)$$

and the fitness of partner 2 is

$$(1 - s)B(u_1 + u_2) - K_2(u_2). \quad (2)$$

The best choice of effort of each female depends on the effort expended by her partner, and consequently we must search for an evolutionarily stable partner effort strategy. McNamara et al. (2003) show that the evolutionarily stable strategy (ESS) depends on the "bidding" process whereby the partners settle on the effort each will expend. They consider four bidding scenarios, but here we use the "single sealed bid" approach, which assumes (i) that each partner submits a bid in advance, (ii) that each has knowledge of the other's bid, and (iii) that each adheres to the bid made. This was first developed by Houston and Davies (1985), on whose work the model of McNamara et al. (2003) is based. We consider in "Discussion" how other bidding scenarios may affect the ESS.

To find the stable effort levels, we first define the "best response function," denoted as R . The best response function $R_1(s, u_2)$ describes the fitness-maximizing bid (effort) of partner 1 when skew is s and partner 2 bids effort u_2 . Analogously, the best response function $R_2(s, u_1)$ describes the fitness-maximizing bid of partner 2 when skew is s and partner 1 bids effort u_1 . (The term "best response function" is misleading in that it suggests to some that the partner's bid is known before a female makes her own bid. In the terminology of McNamara et al. [2003], which we use here, "response" refers to an evolutionary rather than a behavioral response.) The best response of partner 1 can be found by differentiating expression (1) with respect to u_1 and setting the result equal to 0. We obtain

$$sB'[R_1(s, u_2) + u_2] = K'_1[R_1(s, u_2)]. \quad (3)$$

Analogously, the best response of partner 2 can be found by differentiating expression (2) with respect to u_2 and setting the result equal to 0, which yields

$$(1 - s)B'[u_1 + R_2(s, u_1)] = K'_2[R_2(s, u_1)]. \quad (4)$$

In both cases, the result means that the best evolutionary response to a bid of given effort from the partner has the property that the marginal benefit of an increased bid is exactly offset by the marginal cost.

To obtain numerical solutions, we used the functions employed by McNamara et al. (2003). These functions and the calculations are summarized in table 1. Inserting the benefit and cost functions from table 1 in equations (3) and (4), we find in $u_1 - u_2$ space the best response lines

$$R_1(s, u_2) = \frac{1 - u_2}{1 + k_1/s} \quad (5)$$

and

$$R_2(s, u_1) = \frac{1 - u_1}{1 + k_2/(1 - s)}. \quad (6)$$

The intersection of these lines occurs at $\{1/(1 + k_1/s), 1/[1 + k_2/(1 - s)]\}$. At this point neither partner could unilaterally benefit by a different bid. It is a Nash equilibrium and also an ESS (McNamara et al. 2003). This intersection point therefore gives the evolutionarily stable efforts of partners 1 and 2, respectively, under the single sealed bid scenario, for given skew s and body conditions k_i .

Model Predictions

To derive predictions, we used the above procedure to calculate the best effort and fitness of both partners in a coalition for all skews between 0 and 1, in increments of 0.02. We also computed the fitness-maximizing effort and the fitness each partner would expect if lone tending, by using the above procedure and fixing the partner's effort at 0. (There is no skew for lone tenders.) We identified a coalition as possible only at those skew values for which coalition fitness exceeded that from lone tending for both hens, with the reasoning that coalitions form only when they are in the interests of both partners (Öst et al. 2003b). A coalition is no longer advantageous when further increases in skew lower coalition fitness below that expected from lone tending; this is called the reserve position. The overlap in skew values (if any) between the reserve positions of the two hens is the range of skews potentially acceptable to both coalition partners. (There is at present no method agreed upon to predict which particular com-

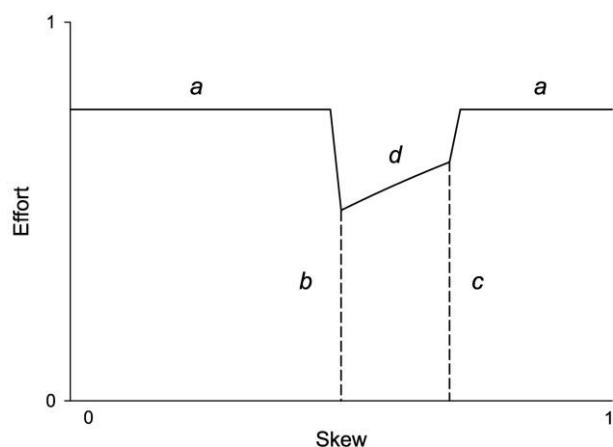


Figure 1: Basic form of the results, showing the best effort of one of the hens (partner 1) as skew is varied from 0 (maximally skewed in favor of partner 2) to 1 (maximally skewed in favor of partner 1). Effort of each hen can range from 0 (none) to 1 (maximum). There are four main features: the height of the line segments *a* is the fitness-maximizing effort of the hen as a lone tender, over the range of skews at which one or both of the partners prefers lone tending to forming a coalition. As the skew improves beyond a threshold *b*, a coalition becomes increasingly beneficial for partner 1, but if skewed beyond *c*, it is no longer attractive for partner 2. Skew levels *b* and *c* are the “reserve positions” of partners 1 and 2, respectively. The line segment *d* gives the stable effort of partner 1 in the coalition. Predictions for partner 2 are not shown but assume the same general form, though the heights of *a* and *d* would depend on the hen’s condition, and *d* would have negative slope.

combination of skew and effort would be selected between the reserve positions of the prospective coalition partners.) The form of our results is shown in figure 1, showing the best effort of (one of) the partners as skew is varied from 0 to 1.

Model Results

Our basic predictions derive from calculations for three sample coalitions: (*a*) two partners, both in good condition ($k_1 = k_2 = 0.5$); (*b*) a good-condition hen ($k_1 = 0.5$) with a medium-condition partner ($k_2 = 1.0$); and (*c*) a good-condition hen ($k_1 = 0.5$) with a poor-condition partner ($k_2 = 2.0$). These three sets of computations are illustrated in figure 2, using the format outlined for figure 1 to display the ESS efforts of a good-condition hen and her good- (fig. 2A), medium- (fig. 2B), or poor-condition (fig. 2C) partner. These results make three general predictions about effort in coalitions that we are able to test with data (see “Results”).

We consider first the fitness-maximizing effort of lone-tending hens in relation to the stable effort level that the same hen would display in a coalition. All six hens (three pairs) in figure 2 demonstrate lower effort in a coalition

than when lone tending. In all situations, this holds for the full range of skews for which a coalition is advantageous.

The second prediction concerns the stable effort in a coalition in relation to body condition. By comparing the good-, medium-, and poor-condition partners (fig. 2A–2C, respectively), it can be seen that the effort devoted by a hen is positively related to her body condition.

The third and final prediction concerns the stable effort of a hen in relation to her partner’s body condition. By comparing the effort of the good-condition hen with good-, medium-, and poor-condition partners (fig. 2A–2C, respectively), it can be seen that the effort devoted by a hen is negatively related to her partner’s body condition. In the remainder of this article, we describe the field procedures and the data collected to test these predictions.

Methods

Data Collection

We observed breeding eiders at Tvärminne Zoological Station (59°50’N, 23°15’E), on the Baltic Sea in southwestern Finland during 2000 and 2002–2004. Eider females were captured on the nest on selected islands in the study area during the late stages of incubation in order to minimize nest desertion from trapping (Kilpi et al. 2001). Females were given, attached to the third-outermost primary, 3 × 3-cm temporary wing flags with a unique color combination (Öst and Kilpi 2000) and a unique combination of one to three permanent color rings (2002–2004). Trapped females were weighed to the nearest 10 g on a Pesola spring balance, the length of the radius-ulna was measured to the nearest 1 mm, and clutch size was recorded. Altogether, 525 females were marked with flags during the study period (2000: $n = 134$; 2002: $n = 124$; 2003: $n = 134$; 2004: $n = 133$). One person (M. Kilpi) conducted all the measurements in order to avoid inter-observer variance.

Females do not eat during incubation and therefore lose weight. To estimate a hen’s weight at hatching of the young, we subtracted an estimate of the weight she would be expected to lose during the remaining incubation time from her measured incubation weight. Each female was weighed only once, but because we captured females at different times in their incubation (see below), we can get a reliable estimate of average weight loss rate during incubation as the slope of the regression of $\log(\text{body weight})$ on $\log(\text{incubation time})$, taking into account year, type of nesting island, and a slight nonlinearity in their arithmetic relationship (Kilpi and Lindström 1997; Öst 1999). The incubation stage was estimated directly from known hatching dates or laying dates or indirectly by an egg floatation

Table 1: Details of the skew model and calculations based on it

	Partner 1	Partner 2	Range
Parameters:			
Share of total benefit (skew)	s	$1 - s$	$0 \leq s \leq 1$
Condition	k_1	k_2	$0 < k_i < 3.0^a$
Variables:			
Effort	u_1	u_2	$0 \leq u_i \leq 1$
Functional forms:			
Benefit	$B(u) = 2u - u^2$	$B(u) = 2u - u^2$	
Cost	$K_1(u_1) = k_1 u_1^2$	$K_2(u_2) = k_2 u_2^2$	
Fitness	$sB(u_1 + u_2) - K_1(u_1)$	$(1 - s)B(u_1 + u_2) - K_2(u_2)$	
Coalitions:			
Best response function	$R_1(s, u_2) = (1 - u_2) / (1 + k_1/s)$	$R_2(s, u_1) = (1 - u_1) / [1 + k_2/(1-s)]$	
Stable efforts	$1/(1 + k_1/s)$	$1/[1 + k_2/(1-s)]$	
Lone tenders:			
FitnessK	$B(u_1) - K_1(u_1)$	$B(u_2) - K_2(u_2)$	
Fitness-maximizing effort	$1/(1 + k_1)$	$1/(1 + k_2)$	

Note: The joint benefit and individual cost functions are those used by McNamara et al. (2003).

^a Low k_i means high condition.

test (Kilpi and Lindström 1997). The difference in the incubation stage as estimated by egg floatation and the real incubation stage as determined by direct observations of laying or hatching is nonsignificant (Kilpi and Lindström 1997). Female condition indices were derived as the standardized residuals of actual estimated body weights at hatching from those predicted from regressions of $\log(\text{body weight})$ on $\log(\text{length of radius-ulna})$ (Ormerod and Tyler 1990). Standardized residual weights at hatching were derived separately for each year.

In 2002–2003, ducklings of known females were marked with both an individual and a brood-specific identification tag (Öst and Bäck 2003). Because the short durability of tags precluded rigorous assessments of the identities of all ducklings in mixed broods (Öst and Bäck 2003), we were unable to test predictions about reproductive skew, confining ourselves to testing predictions about parental effort in coalitions of brood rearing females.

We located individually known females for at least 30 days after hatching of the young, from late May to mid-July. At each sighting of a female we recorded her identity, whether she was attending a brood, and the total number of females and ducklings in the brood. Each focal brood was followed long enough to ensure correct assessment of the brood rearing status of all females attending the brood (Öst et al. 2003b). All observations of a known female during a single day constituted one observation. For a brood rearing focal female, we recorded total observation time, type of activity (seven categories; Öst et al. 2002), and activity duration. In 2000, we used continuous focal-animal sampling to estimate female time-activity budgets (Öst et al. 2002), whereas in 2002–2004, we conducted

scan samples (Altmann 1974) of female activities at 30-s intervals. We found no annual differences in the proportion of time females spent vigilant (arcsine transformed; one-way ANOVA, $F = 0.26$, $df = 3, 211$, $P = .86$), our measure of parental effort, and within-year variances were homogeneous (Levene test, $F = 0.72$, $df = 3, 211$, $P = .54$). Therefore, the potential bias caused by pooling of data collected with two different methods is likely to be negligible.

Data Selection

We used the proportion of time females spent vigilant as our measure of parental effort. This antipredator behavior is a major activity of brood rearing eider females (Öst et al. 2002) and inevitably interferes with a female's need to recover body reserves by diving for food (e.g., Pöysä 1987). It is also less sensitive to subjective bias than other attributes related to parental effort (Öst et al. 2003a).

To maximize observation time, we pooled data from several days (observation units) on a focal marked bird, provided that the age of the focal hen's young did not differ by more than 7 days among the pooled observations. In case there was more than one such pooled observation, we selected the first pooled observation, since the sooner the observation was made, the less the body condition of the focal hen was expected to deviate from our estimate of body condition at hatching of the young. Since the brood characteristics could change during the pooled observation period, we used medians of the number of ducklings and females in the brood. To give a fair representation of female time-activity budgets, we excluded broods ob-

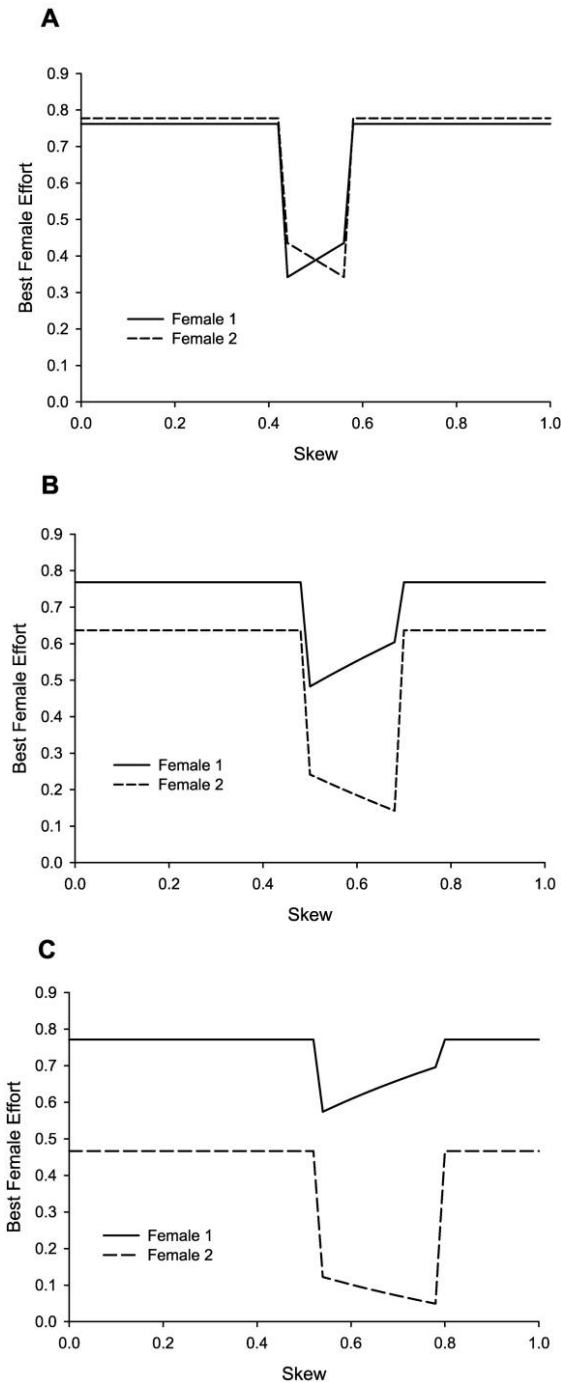


Figure 2: Evolutionarily stable strategy effort levels of partners in three sample coalitions. *A*, Two good-condition ($k_1 = k_2 = 0.5$) partners. *B*, A good-condition hen ($k_1 = 0.5$) with a medium-condition partner ($k_2 = 1.0$). *C*, A good-condition hen ($k_1 = 0.5$) with a poor-condition partner ($k_2 = 2.0$). Each panel is read as is figure 1, except that both partners are portrayed. Partner 1 is represented by the solid line; skew increases in her favor from left to right. Partner 2 is represented by the dashed line; skew increases in her favor from right to left.

served for less than 5 min in total. After pooling of the data, the mean observation time \pm SD per bird was 76.6 ± 56.4 min ($n = 215$).

All data were included when comparing the parental effort of lone tenders and females in coalitions (prediction 1). When we scrutinized the parental effort of females within coalitions (predictions 2, 3), data from 2000 was excluded, to ensure that different methods of observing time-activity budgets (see above) did not bias our results. When we compared the parental effort of at least two known females in the same brood, however, the three cases from 2000 were included, to offset the limited sample size ($n = 27$ broods). This subset of data exclusively consists of females in enduring coalitions with each other (Öst et al. 2003b), that is, coalitions in which the two or more individually known females and their ducklings had consistently associated over a period of at least 2 weeks. Data on several known females in the same brood were further restricted so that only simultaneous observations of the behavior of all known females were included, thus ensuring that all females were exposed to similar conditions at the time of observation. In coalitions with at least two known birds, the mean observation time \pm SD per bird was 100.2 ± 68.0 min ($n = 58$), with no difference between the better-condition (99.8 ± 67.3 min, $n = 35/27$ broods) and poorer-condition coalition partners (102.0 ± 65.6 min, $n = 35/27$ broods; paired t -test, $t = 1.30$, $df = 34$, $P = .20$).

Statistical Analysis

Data were checked for adherence to statistical assumptions before analysis. Proportions of time spent vigilant were arcsine transformed when this improved normality, and the numbers of ducklings and females were log transformed to normalize distributions. Data were analyzed with generalized linear mixed models (GLMMs), executed in S Plus, version 6.1, using the “lme” algorithm (Pinheiro and Bates 1999). This method enables the fitting of random terms and therefore accounts for repeated sampling across error terms. Broods and individuals represented such repeated units of observation. We used a restricted maximum-likelihood (REML) approach (Patterson and Thompson 1971), which is preferable to ordinary maximum-likelihood (ML) procedures when variance components are estimated from an unbalanced design (McCullagh and Nelder 1991).

The Akaike Information Criterion (AIC; Akaike 1973) was used as a guideline for model selection. When we compared models with an identical fixed-effects structure, AIC values were calculated from REML models, whereas comparisons of models differing in their fixed-effects structure were based on ML estimation, to make comparisons of AIC values meaningful. However, all final models reported here refer to REML models. Finally, we

also used likelihood ratio tests (analysis of deviance) to statistically determine which of the alternative preferred models provided the better fit (Crawley 2002).

Before fitting mixed models on the fixed effects of interest, we chose the random effect structure that best fitted our data: brood, female identity, or female identity nested within brood, assuming that these random effects were independent of each other (i.e., had a diagonal variance-covariance structure).

We included a set of variables that may influence the proportion of time females spent vigilant in the overall data on coalitions of brood rearing females. This was done to confirm that the variable of interest, female body condition, had an independent effect on parental effort when other factors potentially affecting parental effort were already accounted for. We included the following independent variables in our GLMM: reference female's body condition; total number of females and ducklings in the brood; reference female's clutch size, based on the number of viable offspring in the nest at the time of marking them (if the brood had already left the nest, all ducklings were assumed to have hatched); and year (categorical). We also added a fifth derived variable into the model: the proportion of reference female's clutch to the total number of ducklings in the brood. Since these proportions typically fell between 0.3 and 0.7, the arcsine transformation was not applied (Sokal and Rohlf 1995), and the untransformed variable more closely resembled a normal distribution. Because of duckling mortality, this variable can give only a rough indication of the focal female's reproductive share of the amalgamated brood. Since year proved to be highly uncorrelated with the dependent variable in all analyses, it is omitted from the models reported here. We also tested for all two-way interactions in the presence of the main effects, but none of these interactions improved the fit of models as judged by the AIC, and so they are not included in the results.

The data on at least two known females in the same brood consisted of 58 females in 27 broods (23 broods with two known birds, four broods in which all three females were known). This yields 35 pairwise comparisons of parental effort within coalitions, whereas in reality there were only 27 totally independent samples. To account for this, partner body condition (good condition/poor condition) was nested within the random effect brood in the corresponding GLMM analysis, thus ensuring that the appropriate degrees of freedom were used in statistical testing.

Results

Prediction 1: effort in a coalition lower than when alone, controlling for parental condition. We ran GLMMs on the

time spent vigilant by lone tenders and females in coalitions, after including brood as the random effect, since such models provided a significantly better fit than models including female identity as the random effect (analysis of deviance on REML models, all $P < .05$), and, judged by the AIC, they were also more parsimonious than models including female identity nested within brood as the random effect, although not significantly so (analysis of deviance on REML models, all $P > .05$). Lone tenders spent a larger proportion of time vigilant than females in coalitions (GLMM, $F = 7.91$, $df = 1, 31$, $P < .01$; fig. 3A). This difference was also upheld after including both female category and female body condition at hatching of the young as fixed effects in the model (GLMM, $F = 7.93$, $df = 1, 31$, $P < .01$; fig. 3B). We conclude that effort in a coalition is lower than when alone, even after controlling for parental body condition.

Prediction 2: effort in a coalition positively correlated with body condition. We first consider the effect of body condition on parental effort in the data on all coalitions in 2002–2004. Here, female identity was chosen as the random effect in modeling, since such models were consistently more parsimonious according to the AIC than models based on alternative random effects, although differences in model fit were not significant (analysis of deviance on REML models, all $P > .05$). A simple model consisting of only the fixed effects female body condition and proportion of reference female's clutch to total number of ducklings provided the best fit to the data (AIC [ML model] = -66.09). However, we here present the best three-factor model also including the number of females as a fixed effect (AIC [ML model] = -64.68), since the proportion of time spent vigilant by individual females has previously been shown to be negatively correlated with female group size (Öst et al. 2002), and the fit of these two top-ranking models did not differ significantly from each other (analysis of deviance, $D = 0.59$, $P = .44$). The overall GLMM for the proportion of time a focal female spent vigilant in a coalition (arcsine transformed) was vigilance = $0.64 + 0.044 \times$ body condition $- 0.059 \times$ log (females) $+ 0.18 \times$ proportion of own clutch. The proportion of time spent vigilant by a focal female increased with her body condition ($F = 4.59$, $df = 1, 17$, $P = .047$; fig. 4) and the proportion of her clutch to the total number of ducklings ($F = 9.78$, $df = 1, 17$, $P < .01$), but it showed a nonsignificant tendency to decrease with number of females in the brood ($F = 2.53$, $df = 1, 17$, $P = .13$). Neither the focal hen's own clutch size nor the total number of ducklings in the joint brood had significant effects in any models, and inclusion of these factors resulted in less parsimonious models. To conclude, female body condition at hatching of the

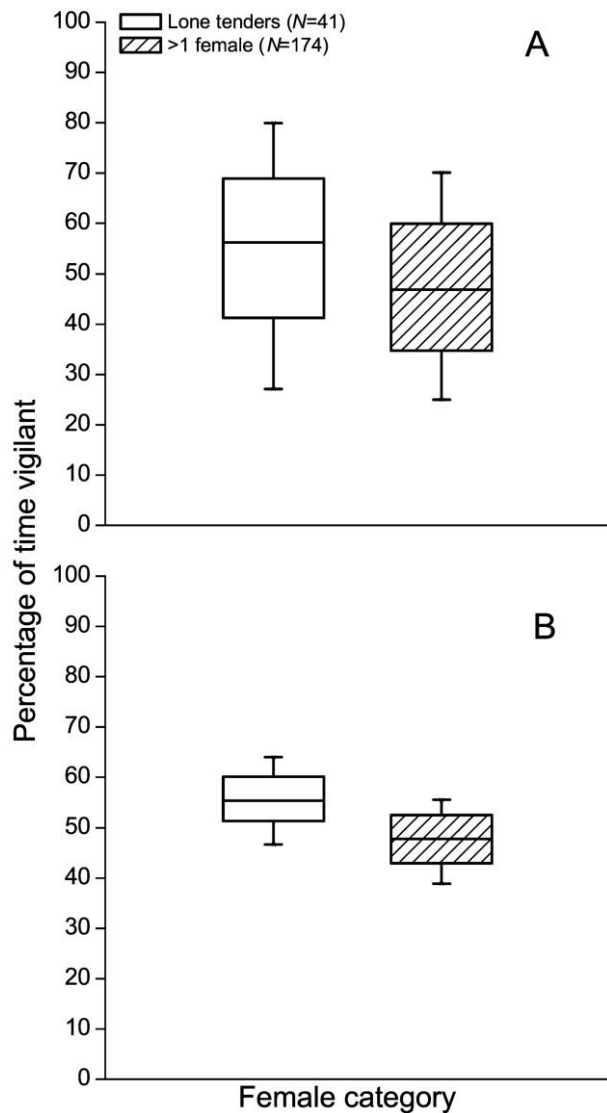


Figure 3: Percentage of time spent vigilant by lone tenders and females in brood rearing coalitions. *A*, Untransformed data; *B*, fitted values from a generalized linear mixed model including female body condition at hatching of the young as a covariate (random effect = brood identity). The top and bottom of the box are drawn at the upper and lower quartiles, the box is divided at the median, and the vertical lines show the tenth and ninetieth percentiles.

young has an independent positive effect on the parental effort of females in coalitions.

This outcome also holds true for females within a coalition. Figure 5 shows the relationship between body condition and parental effort of individually known coalition partners. This pairwise design of parental effort within coalitions was analyzed with a GLMM with brood identity as a random effect and female body condition (good con-

dition/poor condition) nested within brood. The better-condition coalition partner spent a larger proportion of time vigilant than the poorer-condition coalition partner ($F = 6.81$, $df = 1, 26$, $P = .01$). This result is consistent with our prediction that parental effort in a coalition should be positively correlated with body condition.

Prediction 3: effort in a coalition depends on partner condition; effort increases when partner condition decreases and decreases when partner condition increases. This prediction can be reformulated as follows: the residual parental effort of a female, as determined by important predictors of effort (body condition, proportion of own clutch, number of females), should be negative when the female is paired with a better-condition partner and positive when she is paired with a poorer-condition partner. To test this prediction, we selected broods in which the body conditions of all females were known and identified the female in best and poorest body condition. We then compared the residual investment in vigilance of these two categories of females (normalized residuals) with that predicted from a GLMM with body condition, proportion of own clutch, and number of females as fixed effects and female identity as random effect (see prediction 2, above). Brood identity was included as a random effect in the final GLMM anal-

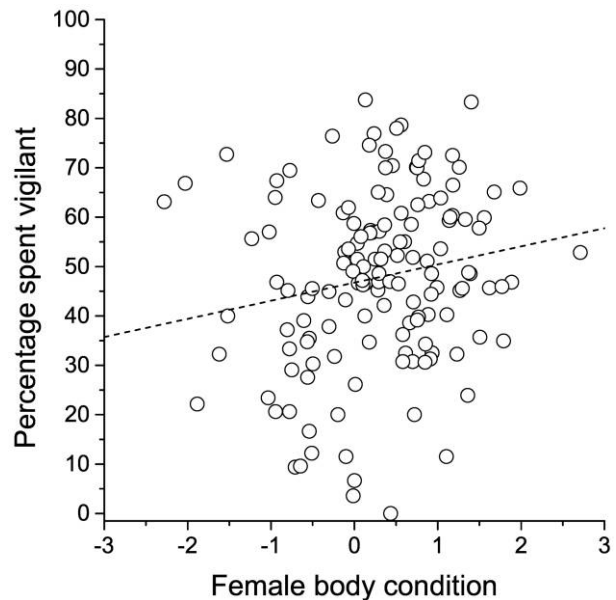


Figure 4: Percentage of time devoted to vigilance by females in brood rearing coalitions as a function of their body condition at hatching of the young. The dashed line indicates the linear regression equation fitted to the data for illustrative purposes only. Untransformed data are shown. The proportion of the female's clutch to the total number of ducklings in the amalgamated brood and the number of females also affect female vigilance (see text), which partly explains the large variation in the data.

Discussion

Testing the Model Predictions

The value of our parental effort model lies in explaining the stable allocation of parental effort in groups in which all individuals are able to reproduce freely; this question has so far received little direct attention from theoreticians compared to systems characterized by dominant control of reproduction (cf. Kokko et al. 2002). Our model is also one of the first to explicitly consider the crucial role of differences within a sex, since most models of parental effort have made the unrealistic assumption that all members of a given sex are equal regarding their cost-benefit functions (cf. Houston et al. 2005).

We have made the assumption that female body condition is determined primarily by unpredictable environmental factors such as breeding weather conditions, choice of nest site, and food supply before nesting. However, some recent studies have revealed a significant additive genetic component of variance in body condition (e.g., Merilä et al. 2001). We therefore need to evaluate how much of the variation in body condition is really due to environmental variation, as opposed to variation in individual “quality” (genetic effect). To this end, we analyzed the body conditions at hatching of the young of all 901 females ($n = 1,350$

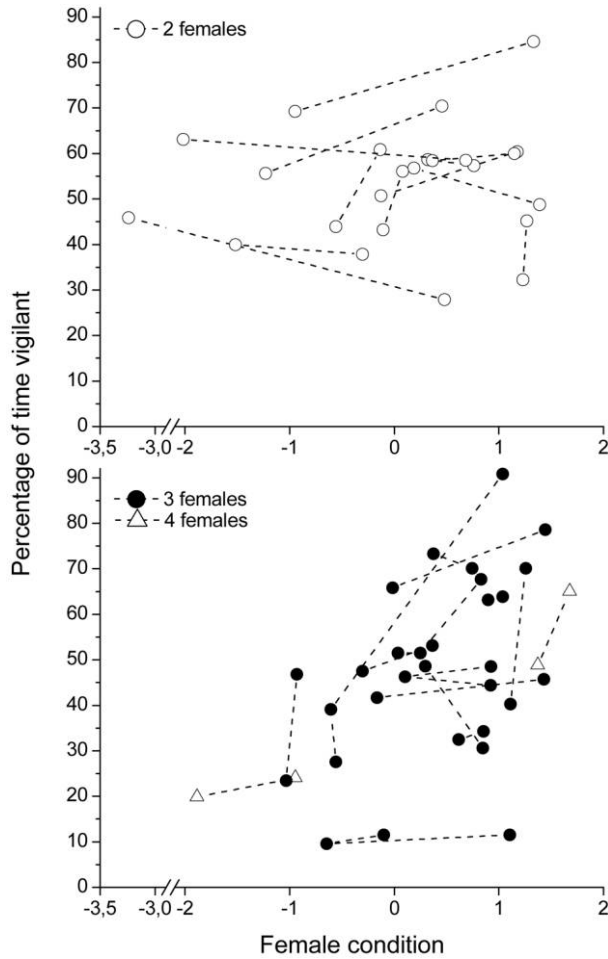


Figure 5: Relationship between body condition and proportion of time spent vigilant of individually known partners in enduring brood rearing coalitions, in which the two or more individually known females and their ducklings had consistently associated over a period of at least 2 weeks. Data from the same brood are connected with a dashed line. The upper panel shows coalitions with two females, the lower panel coalitions with three or four tending females.

ysis. This GLMM analysis showed a nonsignificant tendency for females to have a lower residual investment in vigilance when paired with better-condition partner(s) (mean normalized residual \pm SD = 0.0071 \pm 0.44) compared to females paired with partner(s) in poorer condition (mean normalized residual \pm SD = 0.27 \pm 0.74; $F = 3.20$, $df = 1, 13$, $P = .09$; fig. 6). Given the limited sample size (14 broods) and variation inherent to the data, nonsignificant results are not surprising; given an acceptable power of 0.8 and $\alpha = 0.05$, the required sample size to detect statistically significant differences should be \sim 83 observed broods.

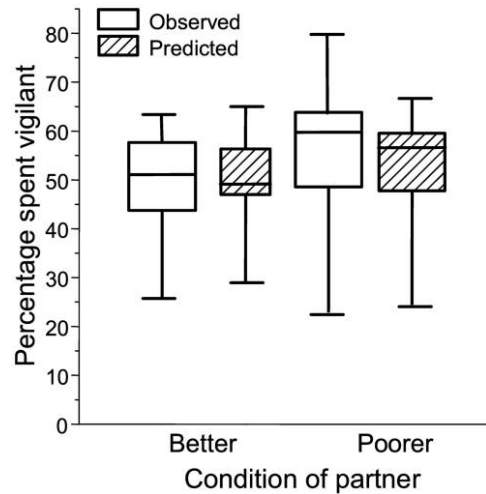


Figure 6: Relationship between the observed time spent vigilant and that predicted by a generalized linear mixed model (fixed effects = body condition, proportion of own clutch, and number of females; random effect = female identity) for females paired up with a better-condition or a poorer-condition partner. There is a marginally significant trend for residual investment in vigilance to be higher for birds forming coalitions with poorer-condition partners as compared to birds pairing with better-condition partners (see text). The top and bottom of the box are drawn at the upper and lower quartiles, the box is divided at the median, and the vertical lines show the tenth and ninetieth percentiles.

observations) trapped in 1996–2005. We performed a variance component analysis of the body condition data based on a GLMM with female identity as a random effect and the overall mean as the only fixed effect (Crawley 2002). Within-individual variation in body condition among years was high ($s^2 = 0.595$), accounting for 59.1% of the total variation, whereas between-individual variation was relatively modest, accounting for the remaining 40.9% of the variation ($s^2 = 0.413$). Thus, our assumption that environmental contributions to body condition are likely to be more important than individual (genetic) effects is justified. In line with this conclusion, individual common eider females change their general mode of parental care between years, and this variation in turn reflects variation in their body condition (Kilpi et al. 2001).

Our basic predictions were derived from a simple model that considered the interaction of two females. The interactions probably become more complex and potential outcomes more variable as the number of caretakers increases (e.g., Sozou and Houston 1994; Hatchwell 1999), and a model with three or more interactants would be correspondingly complicated. We did not develop such a model here, but the underlying assumptions and hence the strategic logic explaining why a female's effort depends on her condition relative to that of her partners should remain intact when there are multiple partners. Specifically, hens may improve their brood's prospects (and hence fitness) by partnering with other females, but because poor-condition hens have poor prospects as lone tenders, they are willing to accept a wider range of skews than are good-condition hens. Extra effort is also more expensive for poor-condition hens, leaving those in good condition with most of the strategic options.

Our data support the first prediction that the stable effort of a female should be lower when in a coalition as opposed to tending alone, given that body condition is kept constant. This finding agrees with the general picture emerging from the much wider literature on sexual conflict over parental effort; a member of a pair will compensate for the absence of its mate by working harder (McNamara et al. 2003). An attendant question is how the level of parental effort by a single parent compares with the total effort of a pair. In biparental species, in which parental investment rules are confounded by sexual differences, the results are mixed: most studies report that the level of care provided by single parents is either less than or equal to the total care provided by a pair (McNamara et al. 2003), but the total biparental care may even fall below that of single parents (Royle et al. 2002). Based on our previous data (Öst et al. 2002), the collective vigilance of common eider females in coalitions was at least 20% higher than the vigilance of lone tenders. Nevertheless, a study from a Norwegian common eider population suggested that duckling

survival in two-female coalitions was similar to that of lone-tender broods (Bustnes and Erikstad 1991). Theoretical work suggests that biparental care is unstable if one parent can raise the young nearly as successfully as both parents, and the energetic costs of uni- and biparental care are the same, as has been suggested for species with precocial, less demanding offspring (Barta et al. 2002). We believe, however, that the assumption of roughly equal costs of uni- and multiparental care does not hold for common eiders. Grouping benefits may mitigate the costs of caring for post-incubating, energetically stressed females because individual females feed more but are less vigilant when the number of caring females in the brood increases (Öst et al. 2002).

We also found support for the prediction that the parental effort devoted by a hen is positively related to her body condition. This prediction was upheld in the overall data on all observed broods, and, more importantly, it also held true for individual females within the same brood. Our result demonstrates the danger of treating all members of the same sex as identical regarding their cost-benefit functions of parental investment (Houston et al. 2005). Body condition affects mainly the costs of parental effort in our model; whereas the benefits to each parent depend on the combined effort of all hens, the costs depend only on the hen's own effort, and hens in good body condition are expected to pay a lower cost for a given level of effort (cf. Cant and Field 2005). Providing a high level of care may have a detrimental effect on female survival prospects by reducing fat reserves because of a reduction in the time available for feeding. Unfortunately, we lack data from our population on how quickly postincubating eider females are able to regain their body condition and whether there are any carryover effects of poor body condition on subsequent survival. However, in a common eider population from Norway, it was found that females laying smaller clutches, presumably birds in poorer condition, had a slightly lower survival than females laying larger clutches (Yoccoz et al. 2002). There is also some evidence from related species that poor body condition may have long-lasting repercussions—in barnacle geese (*Branta leucopsis*), female geese with experimentally lowered body condition started the winter migration with smaller reserves than either unmanipulated females or females with experimentally enhanced body condition (Tombre and Erikstad 1996).

Our last prediction, that the effort devoted by a female should be negatively related to her partner's body condition, implies that a female is capable of facultative adjustments of her parental effort not only according to her own condition but also according to her partner's condition, which in turn is reflected on her parental effort. We found some support for this, since females tended to show a higher residual investment in vigilance when paired

with poorer-condition partner(s) than when paired with partner(s) in better condition. This result agrees with studies conducted on biparental species; with two notable exceptions (Dearborn 2001; Hinde 2006), matched responses to changes in partner parental effort have not been observed. A closer examination of our data (fig. 6) reveals an interesting pattern: females paired with better-condition partners did not seem to show a negative residual investment in vigilance as compared to that predicted by their body condition, proportion of their own clutch, and the number of females in their coalition (see “Results,” prediction 3). Females investing less in antipredator vigilance may be subject to agonistic interactions by their coalition partners because female eiders form dominance hierarchies (e.g., Öst 1999). Although all females are free to leave the group and care for their brood on their own, females in poor condition may be less inclined to do so because of the poor survival prospects of their young (cf. Öst et al. 2003b) and may therefore adjust their level of vigilance accordingly to comply with their coalition partners’ demands. Individuals often have to compromise their own activity budgets to avoid social costs such as intra-group aggression and the risk of eviction (Johnstone and Cant 1999; Crespi and Ragsdale 2000).

The commonly observed “group-size effect” on vigilance, with individual levels of antipredatory vigilance declining with group size (e.g., Roberts 1996), could also explain our

first prediction. Group-size effects on vigilance have been modeled almost exclusively in the context of personal predation avoidance, and outside this context, the relationship between vigilance and group size is poorly understood (Beauchamp 2001). The protection of ducklings from predation by gulls is the main function of amalgamated broods in common eiders. Hence, because vigilance should be regarded as parental care rather than female predation avoidance, the parental care game approach used by us may be considered a more appropriate theoretical framework. Furthermore, no antipredatory group-size models of vigilance have so far incorporated the effect of variable condition of group members in order to generate general predictions about their individual level of vigilance. Consequently, these group-size models are inadequate for predicting the stable level of effort of a focal female in a brood rearing coalition in relation to her own (prediction 2) or her partner’s body condition (prediction 3).

Do Eider Hens “Negotiate” Skew and Effort?

We used the single sealed bid approach of McNamara et al. (2003) to calculate the stable efforts of a pair of partner hens for all the skews possible in any particular coalition (see “Partner Effort Model”). These calculations, summarized in table 1, form the basis of our predictions about the relative effort of the hens. McNamara et al. (2003)

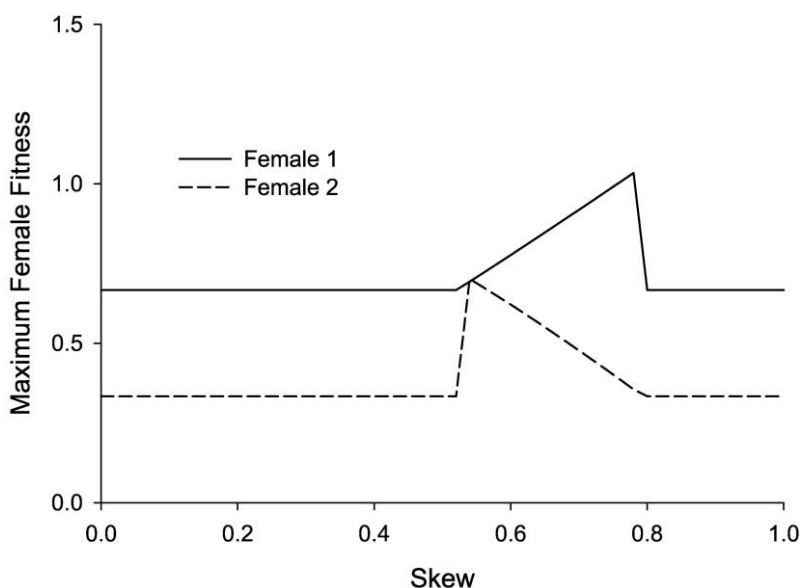


Figure 7: Fitness (arbitrary units; defined by eqq. [1], [2]; see also table 1) of the partners in the coalition portrayed in figure 2C (a good-condition hen [$k_1 = 0.5$] with a poor-condition partner [$k_2 = 2.0$]). Note that a hen’s effort (shown in fig. 2) and fitness (shown here) both rise as the structure of the joint brood is skewed in her favor. Partner 1 is represented by the solid line; skew increases in her favor from left to right. Partner 2 is represented by the dashed line; skew increases in her favor from right to left.

analyze this and three other bidding scenarios with various assumptions (Stackelberg game: one partner bids first; cooperative: partners maximize joint gain; negotiation: efforts are chosen after a cost-free period of repeated bidding) and discuss their effects on the stable effort levels.

However, understanding which of the skew-effort combinations the hens settle on presents issues beyond choosing one of these bidding scenarios. In figure 7 we calculate the fitness of the partner hens whose stable efforts are shown in figure 2C. The figure illustrates that each hen attains higher fitness when the skew is in her favor (even though the stable effort is higher), suggesting that each would prefer to skew the structure of the joint brood in her own favor. Even if we assume that one of the partner effort games described above is adequate to predict effort in relation to a given skew, it remains unclear how the skew is settled. Models of skew have generally assumed that a dominant individual is able to control the allocation of benefits (Johnstone 2000), so it is not necessary to consider negotiation or bargaining. Some articles have considered “incomplete control” (Clutton-Brock 1998), but bargaining has not been extensively studied in behavioral ecology.

The natural history of the situation is suggestive of a period of behavioral interaction, during which effort and skew are bargained. For a few days after hatch, eider hens are found in groups of up to more than 10 females, during which they form enduring coalitions with just one or two hens (Öst et al. 2003a), take up lone tending, or abandon their ducklings. Intense socializing and fighting are common during this time but occur only rarely later. Aggression may provide a means to influence the reproductive skew within the group, since a female’s aggression frequency predicts her centrality in brood rearing coalitions (Öst et al., forthcoming) and predation of ducklings by gulls is edge biased (e.g., Swennen 1989). On occasion, nascent coalitions of hens break up after a few days, evidently because the partners are not suited to each other (Öst et al. 2003b). We hypothesize that these behaviors are related to the search for suitable coalition partners and that hens bargain with potential partners about the effort each will allocate and the skew of the joint brood.

To investigate this further, we need to develop methods to measure skew in the field, and we also need to understand the evolution of bargaining behavior. Nash (1950) proposed a “bargaining game” in economics. At the settlement point in a Nash bargain, the marginal gain to one party of a small change is exactly offset by the marginal cost to the other party (Morrow 1994). Young (1993) showed how a population bargaining according to the rules proposed by Nash (1950) will evolve to an ESS. The Nash bargaining solution depends on the “reserve” or “status quo” points as well as on benefit functions. The

natural history of the situation developed here does have obvious reserve points for each bargainer (namely, the skew beyond which a coalition is no longer beneficial), and the benefit functions are in principle measurable. Thus, this model structure would seem to have promise for studying this and analogous situations in behavioral ecology in which individuals with divergent interests have to bargain a settlement.

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