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Clutch-size adjustments and skew models: effects on reproductive partitioning and group stability

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Reproductive skew theory seeks to integrate social and ecological factors thought to influence the division of reproduction among group-living animals. However, most reproductive skew models only examine interactions between individuals of the same sex. Here, we suggest that females can influence group stability and conflict among males by modifying their clutch size and may do so if they benefit from the presence of subordinate male helpers or from reduced conflict. We develop 3 models, based on concessions-based, restraint, and tug-of-war models, in which female clutch size is variable and ask when females will increase their clutch size above that which would be optimal in the absence of male–male conflict. In concessions-based and restraint models, females should increase clutch size above their optima if the benefits of staying for subordinate males are relatively low. Relatedness between males has no effect on clutch size. When females do increase clutch size, the division of reproduction between males is not influenced by relatedness and does not differ between restraint and concessions-based models. Both of these predictions are in sharp contrast to previous models. In tug-of-war models, clutch size is strongly influenced by relatedness between males, with the largest clutches, but the fewest surviving offspring, produced when males are unrelated. These 3 models demonstrate the importance of considering third-party interests in the decisions of group-living organisms. *Key words:* brood size, conflict reduction, dominance hierarchy, male quality, mate choice. *[Behav Ecol 18:467–476 (2007)]*

Societies of group-breeding animals range from despotic, in which one or a few dominant individuals monopolize all direct reproduction, to egalitarian (Vehrencamp 1983a, 1983b). Reproductive skew theory attempts to explain this variation in the division of reproduction within dominance-structured breeding groups in relation to ecological and social variables. In the more than 2 decades since the first optimal skew models were developed (Vehrencamp 1983a, 1983b), numerous variants have been proposed, examining the roles of such factors as relatedness, ecological constraints (e.g., Vehrencamp 1983a, 1983b; Keller and Reeve 1994; Reeve and Keller 1997), dominant control (e.g., Reeve et al. 1998), group augmentation (Kokko et al. 2001), resource inheritance (Kokko and Johnstone 1999; Ragsdale 1999; Cant and Field 2001), or the cost of young on skew (Cant and Johnstone 1999), as well as the relationship between skew and aggression (Cant and Johnstone 2000; Reeve 2000), group size (Hamilton 2000), or reproductive inhibition (Hamilton 2004). Two major groups of skew models have been developed: transactional models (Clutton-Brock 1998; Johnstone 2000; Reeve 2000), which assume that the reproductive shares of dominant and subordinate group members are the outcome of transactions over reproductive division and group membership, and tug-of-war models (or incomplete control models, Clutton-Brock 1998; Reeve et al. 1998; Johnstone 2000), in which reproductive division is the outcome of investment in costly competition by group members. Transactional models can further be subdivided into concessions-based models (Reeve and Ratnieks 1993), in which dominant individuals that can control reproductive division allocate some direct reproduction to subordinates to entice them to stay in the group, and restraint models (Johnstone and Cant 1999), in which subordinates may refrain from reproducing to avoid eviction. These 3 general models describe different social systems, which differ in which individual (if any) controls the division of reproduction and/or group membership (for review, see Johnstone 2000).

Nearly all of the extant skew models only consider interactions between pairs of individuals. Even those that consider larger groups implicitly assume interactions only within one sex. That is, they assume that the division of reproduction among males is not influenced by female choice and vice versa for females. However, females often have substantial control over the distribution of paternity (e.g., spotted hyaenas, *Crocuta crocuta*, East et al. 2003). If subordinate males are helpful in the broadest sense, that is, their presence increases the survival of group-produced offspring, females benefit and, in the logic of transactional models, may be willing to allow subordinate males some direct reproduction. Recently, Cant and Reeve (2002) developed a model incorporating female decisions into a model of reproductive skew among males. Among their predictions was that there would be a zone of conflict over which females would prefer to allocate reproduction to subordinate males whereas dominant males would not.

In some cases, however, females may have little direct control over the division of reproduction or group membership. For example, females may have difficulty avoiding sneakers (Luttbeg 2004). Similarly, if access to the breeding female is strongly influenced by male–male interactions, females may only be able to control paternity by refusing matings. This may be costly in some systems (Clutton-Brock and Parker 1995). Even if a female can allocate reproduction to each mate, she may be unable to prevent dominant males from circumventing that decision by evicting subordinates. Therefore, she may gain from allocating additional reproduction to dominant males to keep them from evicting or departing. Recently,

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females of the cooperatively breeding cichlid, *Neolamprologus pulcher*, were found to increase clutch sizes when male helpers had opportunities to leave the breeding group and breed independently (Heg et al. 2006).

Why females would be able to influence group stability by adjusting clutch size can be seen from 2-player skew models. Group productivity has a strong influence on the division of reproduction within groups and, especially, on the stability of groups. Both concessions and restraint models of skew predict that the dominant male should allow subordinates to stay (by allocating sufficient direct reproduction or by not evicting, respectively) when group productivity is high. Although group productivity is generally thought of as the contribution of subordinates or the benefits of grouping, from the male perspective it does not matter what mechanism leads to larger clutches in groups (except indirectly, through changes in future survival or fecundity of mates). If a female increases her clutch size when breeding with a dominant and subordinate male present, this may have similar effects on dominant and subordinate male decisions as increasing group productivity.

Females may also adjust their clutch size regardless of whether there is a risk of subordinate departure if they can expect help raising offspring or gain other benefits from grouping. Although cooperatively breeding species generally have smaller clutches than solitary breeding taxa (Arnold and Owens 1998; Hatchwell and Komdeur 2000), there is some evidence that, within populations, females with helpers or those who expect greater care produce more or larger young (Craig 1980; Taborsky 1984; Hunter 1985; Kolm 2001). Here, we seek to examine the conditions under which females would increase their clutch size above their own optimum to retain the subordinate or to reduce costly conflict between males. We model concessions-based, restraint, and tug-of-war versions of this scenario.

Table 1
Parameters used in the models

Symbol	
All models	
α	Cost of producing a clutch of one on future female survival
β	Cost of clutch size on survival of current brood
i	Male status (dominant, D or subordinate, S)
m	Scaling constant relating clutch size to future female survival (assumed to be 2)
n_a	Clutch size when breeding as a pair
n_g	Clutch size when breeding in group
q_i	Quality of male i
p	Proportion of direct reproduction obtained by subordinate
r	Relatedness between dominant and subordinate males
s_a	Expected survival of current brood if breeding as a pair
s_g	Expected survival of current brood if breeding in group
y	Quality of subordinate male relative to dominant male
Transactional models only	
h	Effect of help on survival of current brood
x	Probability that subordinate male finds a breeding position if it leaves
Restraint model only	
ε	Direct cost of eviction for dominant
Tug-of-war model only	
b	Subordinate efficiency in converting investment in struggle for reproduction into competitive success in tug-of-war model
d	Dominant investment in struggle for reproduction in tug-of-war model
u	Subordinate investment in struggle for reproduction in tug-of-war model

THE MODEL

In these models, we assume that the decisions of females and dominant and subordinate males are simultaneous, single "sealed-bids." Simultaneous decisions are assumed in most skew models, and by assuming this, we can compare the influence of third-party decisions with the predictions of classical models. We acknowledge that decisions regarding reproductive division, reproductive output, and group membership often will be sequential. Systems likely to meet the assumptions of these models are presented in the Discussion of this paper. Parameters used in the models are listed in Table 1.

Clutch size is often assumed to reflect 2 trade-offs: between current and future reproduction and between number and survival of the current brood (Stearns 1992). As such, a general model for direct fitness as a function of clutch size (n) is

$$w_f(n) = s(n)\sum_i p_i q_i n + f_f(n), \tag{1}$$

$$w_i(n) = p_i q_i n s(n) + f_i(n). \tag{2}$$

In Equation 1, $s(n)$ is the survival of offspring and $f(n)$ is future reproductive success, both of which may decline with increasing clutch size. The quality of each male is denoted by q_i, whereas the proportion of offspring of each male is denoted p_i. To simplify, we consider 2 possible breeding scenarios: pair breeding (i.e., a single male and female) or group breeding with one female and 2 males that differ in social status ($i \in \{D,S\}$ where D is the dominant male and S the subordinate). We refer to the proportion of offspring of the subordinate as p and that of the dominant as $1-p$. Under the simplifying assumptions that male future reproductive success is not influenced by brood size and is the same for group and pair breeding males, the future fitness cost of fathering a large clutch can be ignored for males. We use the following functions to relate clutch size to female and male current and future reproductive success:

$$f_f(n) = 1 - \alpha n^{\mathrm{m}}, \tag{3a}$$

$$f_i(n) = 0. \tag{3b}$$

For simplicity, we assume that m = 2. We used the following survival functions for pair-produced offspring, $s_a(n)$, and group-produced offspring $s_g(n)$:

$$s_a(n) = 1 - \beta n, \tag{3c}$$

$$s_g(n) = (1 - \beta n)(1 + h), \tag{3d}$$

where the value of subordinate help, $h < \beta n$. We assume that h is fixed and depends only on the presence of the subordinate.

For dominant males (i = D), we set $q_{\mathrm{D}} = 1$. The current direct fitness of a dominant male breeding in a pair is

$$w_{\mathrm{D}_a}(n) = n_a s_a(n). \tag{4a}$$

If it breeds in a group with a subordinate male, its current direct fitness is

$$w_{\mathrm{D}_g}(n) = (1 - p) n_g s_g(n). \tag{4b}$$

We set the ratio of subordinate to dominant male genetic quality as $y = q_{\mathrm{D}}/q_{\mathrm{S}}$. Subordinate males that leave the group

may face "ecological constraints" such as predation risk or habitat saturation that prevent them from establishing a breeding territory. Thus, their expected reproductive success is discounted by a factor, x (hereafter referred to as "opportunities for independent breeding"), so that the expected current direct reproductive successes of a subordinate male attempting to breed in a pair and in a group are

$$w_{S_a}(n) = xyn_a s_a(n), \tag{5a}$$

$$w_{S_g}(n) = pyn_g s_g(n). \tag{5b}$$

TRANSACTIONAL MODELS

Concessions-based model

In a concessions-based model, dominant males are assumed to have complete control over reproductive division. However, subordinates can decide whether to remain in the group or to attempt pair breeding. As in the classical concessions-based model, the minimum proportion of reproduction, p, that will entice subordinates to remain in the group is that which equalizes the payoffs to pair and group breeding, that is when

$$w_{S_a}(n) + rw_{D_a}(n) = w_{S_g}(n, p) + rw_{D_g}(n, p). \tag{6}$$

This is so when

$$p^* = \frac{(r + xy)n_a s_a(n_a) - rn_g s_g(n_g)}{n_g(y - r)s_g(n_g)}. \tag{7}$$

When group members are relatives, subordinates may be willing to stay in the group even if they receive no direct reproduction (note that we ignore the possibility of territory inheritance in these models). Staying and receiving no direct reproduction (i.e., $p = 0$) would still yield an equal or greater fitness payoff than leaving when

$$n_g \geq \frac{r(1 + h) - \sqrt{r(1 + h)(r(1 + h) - 4\beta n_a(r + xy)s_a(n_a))}}{2r\beta(1 + h)}. \tag{8}$$

If dominants are willing to concede p^*, the group will be stable. The fitness payoff of retaining the subordinate and yielding p^* will be the same as that of allowing the subordinate to leave when $n_g = n_{\min}$, where

$$n_{\min} = \frac{1 + h - \sqrt{(1 + h)(1 + h - 4\beta n_a(1 + x)s_a(n_a))}}{2\beta(1 + h)}. \tag{9}$$

Given $p = p^*$, dominant fitness increases with increasing clutch size (i.e., $\partial w_D/\partial n > 0$) at $n_{\min}$ when $y > r$. Thus, when this is so, $n_{\min}$ represents the minimum clutch size necessary for group stability. It is likely that the condition $y > r$ will be met in most systems, as variation in genetic quality among males is generally considered to be rather low (see also Cant and Reeve 2002) and should decrease as relatedness between males increases. As in classical skew models, dominant males that permit subordinates to stay should concede exactly p^*.

Female perspective

The optimal clutch size for a female breeding with a single male (n_a^*) reflects the within-clutch and future costs of reproduction. Female fitness when breeding with a single male, $w_a(n_a)$, is found by substituting $n = n_a$ into Equations 1 and 3c. This is maximized with respect to clutch size (i.e., $\partial w_a(n_a)/\partial n_a = 0$ and $\partial^2 w_a(n_a)/\partial n_a < 0$) when

$$n_a^* = \frac{1}{2(\alpha + \beta)}. \tag{10}$$

If a female can expect help raising offspring or other group benefits that increase offspring survival, her fitness, ($w_g(n_g)$), is found by substituting $n = n_g$ into Equations 1 and 3d. Her optimal clutch (i.e., $\partial w_g(n_g)/\partial n_g = 0$ and $\partial^2 w_g(n_g)/\partial n_g < 0$) is

$$n_g^* = \frac{(1 + h)(py + (1 - p))}{2(\beta(1 + h)(py + (1 - p)) + \alpha)}. \tag{11a}$$

If $y = 1$, this becomes

$$n_g^* = \frac{(1 + h)}{2(\beta(1 + h) + \alpha)}. \tag{11b}$$

The maximum clutch size that a female would be willing to produce in a group ($n_{\max}$) is the largest clutch for which group breeding is more profitable than pair breeding (i.e., when $w_g(n_g) = w_a(n_a^*)$). In the simplest case, when $y = 1$ (males are of the same genetic quality), this is when $n_g = n_{\max}$, where

$$n_{\max} = \frac{(\alpha + \beta)(1 + h) + \sqrt{h(\alpha + \beta)(\alpha + (\alpha + \beta)(1 + h))}}{2(\alpha + \beta)(\beta(1 + h) + \alpha)}. \tag{12}$$

Predicted clutch and group sizes

The above thresholds yield 3 possible combinations of clutch and group sizes. First, females may be able to produce their optimal clutch size (n_g^*), and this will be sufficient for subordinate group members to stay in the group (i.e., dominants will allocate p^* to subordinates). This will be the case if $n_{\min} \leq n_g^*$. If the female's optimal clutch size is smaller than $n_{\min}$, she would still do better producing a larger clutch and retaining the subordinate than she would if the subordinate left when $n_{\min} < n_{\max}$. If this is so, a female should produce a clutch of exactly $n_{\min}$ (as a larger clutch would be costly) and subordinates should stay in the group. Finally, a female may do better with just the dominant male than she would by producing $n_{\min}$ and retaining the subordinate (i.e., $n_{\min} > n_{\max}$). In this case, the female should produce n_a^* and the subordinate should leave the group.

The effects of several ecological and social parameters on these thresholds are shown on Figures 1–3. Clutch size is predicted to be at the female optimum when opportunities for dispersal, x, are low and the value of help, h, is high, that is, when the net benefits of group breeding (for subordinate males) are high (Figure 1a,b, respectively). As these benefits decline (i.e., x increases or h decreases), clutch size switches to $n_{\min}$. In this phase, clutch size increases with decreasing net benefits to group breeding. Finally, grouping is not stable when the net benefits to grouping are low. Relatedness between dominant and subordinate males has no effect on clutch size.

Intuitively, high costs of producing a large clutch lead to smaller clutches (e.g., Figure 2). However, these costs also influence group stability. Interestingly, the cost to female future reproductive success influences subordinate male departure from the group even though he does not pay this cost directly (Figure 2a). When this cost is low, subordinate males can expect relatively high success if they leave and attempt to breed independently and dominant males can expect high success if they evict. This is because this cost is assumed to be the same for all females in the population, so that a male

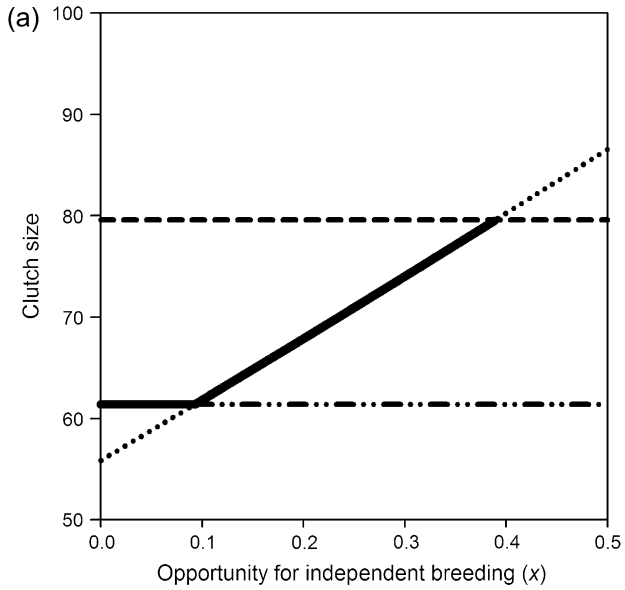

Figure 1
Predicted clutch size in both the concessions-based and restraint transactional skew models depending on (a) the subordinate male's expected probability of finding a breeding territory on leaving the group (x) and (b) the contribution of the subordinate male to juvenile survival (h). The dashed line (▬ ▬ ▬) is the maximum clutch size that the female is willing to produce to retain the subordinate male in the group. The dotted line (▪▪▪▪▪▪▪▪▪▪▪▪) is the minimum clutch size for the dominant and subordinate to both accept group breeding. The dotted/dashed line (▬ ▪ ▬) is the female's optimal clutch size when breeding as part of a trio. The thick, solid black line represents the solution to the model. Note that the predictions for the 2 transactional models are identical only when male qualities are equal ($y = 1$) and eviction is not costly ($\varepsilon = 0$). Other model parameters: $h = 0.05$, $x = 0.4$, m = 2, $r = 0.25$, $\alpha = 0.0075$, $\beta = 0.001$.

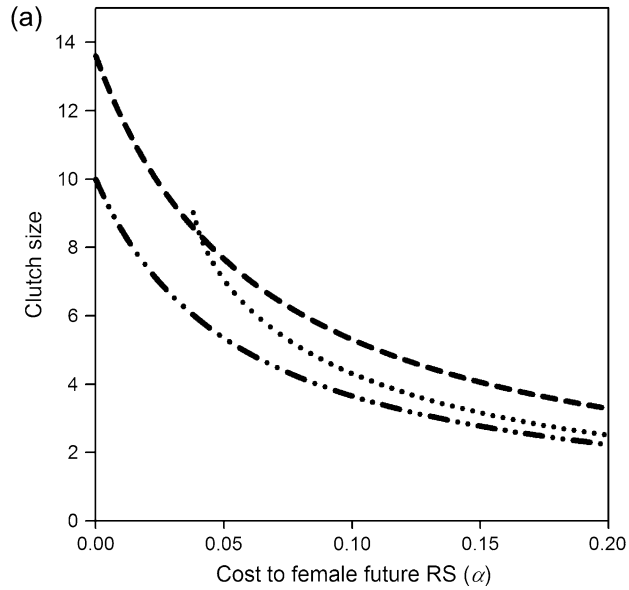

Figure 2
The effects of varying costs of clutch size on model thresholds for both transactional models. (a) Effect of varying the cost to female future reproductive success (α). (b) Effect of varying the cost on current juvenile survival (β). The dashed line (▬ ▬ ▬) is the maximum clutch size that the female is willing to produce to retain the subordinate male in the group. The dotted line (▪▪▪▪▪▪▪▪▪▪▪▪) is the minimum clutch size for the dominant and subordinate to both accept group breeding. The dotted/dashed line (▬ ▪ ▬) is the female's optimal clutch size when breeding as part of a trio. Other model parameters: $x = 0.4$, $h = 0.15$, m = 2, $r = 0.25$, $\alpha = 0.075$, $\beta = 0.001$, $y = 1$, $\varepsilon = 0$.

that leaves the group and does breed independently can expect to attract a female that will produce a large clutch. Not surprisingly, groups are less likely to be stable if the within-clutch competition cost is high (Figure 2b). When this is so, none of the group members have an interest in a large group-produced clutch.

The relative quality of subordinate males also influences the predicted clutch size. In particular, the maximum clutch size that the females will be willing to produce increases strongly with increasing relative quality of subordinates (Figure 3a). This means that groups are more likely to persist when subordinates are of relatively high quality. The optimal clutch size of females also increases, albeit only slightly, with increasing subordinate quality. On Figure 3a, extrapolating the line relating optimal clutch size to subordinate quality, it eventually

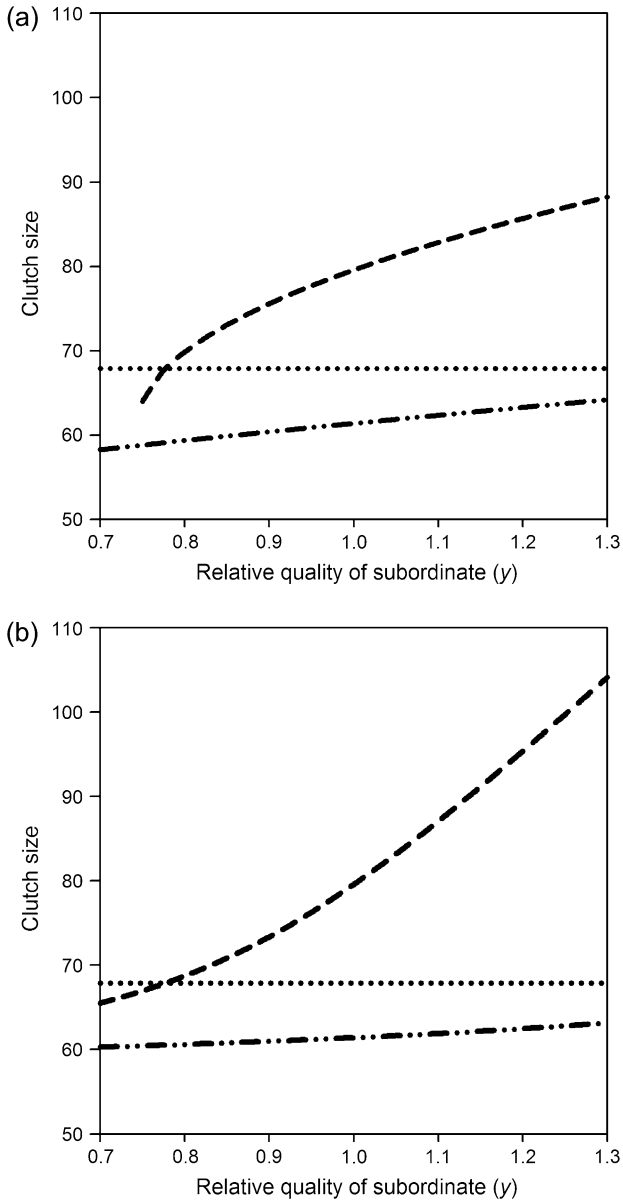

Figure 3
The effect of varying the relative quality of the subordinate male (y) on model thresholds for (a) the concessions-based model and (b) the restraint model. The dashed line (– – – –) is the maximum clutch size that the female is willing to produce to retain the subordinate male in the group. The dotted line (·····) is the minimum clutch size for the dominant and subordinate to both accept group breeding. The dotted/dashed line (— · · —) is the female's optimal clutch size when breeding as part of a trio. Other model parameters: $x = 0.4$, $h = 0.15$, m = 2, $r = 0.25$, $\alpha = 0.075$, $\beta = 0.001$, $\varepsilon = 0$.

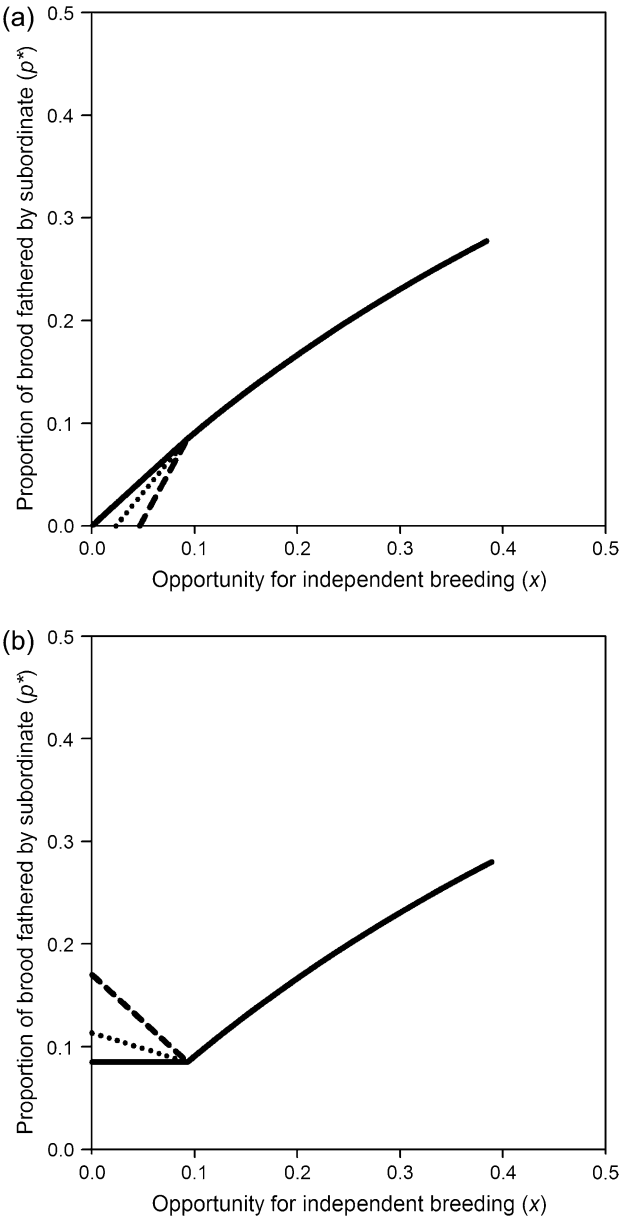

Figure 4
Effects of relatedness between males (r) and opportunities for dispersal (y) on predicted skew (expressed as the proportion of reproduction allocated to the subordinate male) for the (a) concessions-based and (b) restraint models. Clutch sizes for the same parameters are shown in Figure 1.

intersects the subordinate's minimum demand, which is not influenced by its relative quality. In other words, when subordinate males are of high relative quality, the optimal clutch for females may be more likely to exceed that required to keep the group together.

Substituting n_g^* or $n_{\min}$ for n as appropriate into Equation 7, the stable share of direct reproduction allocated to the subordinate is shown on Figure 4. The predicted value of p^* depends on whether clutch size is n_g^* or $n_{\min}$. When clutch size is at the female optimum n_g^*, the general predictions of the classical skew model (Keller and Reeve 1994) hold: p^* increases with increasing opportunities for independent breeding and decreases with increasing relatedness. However, when clutch size is adjusted to retain subordinates in the group (i.e., $n_{\min} > n_g^*$), relatedness has no effect on skew, and predicted skew is equal to that in the classical model when relatedness is 0.

Restraint model

In the restraint model, subordinates decide on the amount of reproduction they will attempt to take from dominants. Dominants decide whether to evict the subordinate. Eviction may be costly to both dominant and subordinate. We include a cost to dominants (ε) (the cost to subordinates can be considered as a part of x). The maximum proportion of reproduction that

subordinates can take from dominants is that which equalizes the payoff to dominants for group and pair breeding. This amount is

$$p^* = \frac{n_g s_g(n_g) - (1 + rxy) n_a s_a(n_a) + \varepsilon}{n_g(1 - ry) s_g(n_g)}. \quad (13)$$

In principle, even if subordinates do not attempt to take any direct reproduction (i.e., $p^* = 0$), they may still be evicted by related dominants because dominants would gain some indirect fitness from independent breeding by subordinates. However, we find that this threshold never influences predicted clutch size in our model.

Groups are expected to be stable if taking a share, p, of direct reproduction yields a higher fitness payoff for subordinates than does independent breeding. The minimum group size at which this is so is

$$n_{\min} = \frac{1 + h - \sqrt{(1 + h)(1 + h - 4\beta n_a(1 + x) s_a(n_a) + 4\beta\varepsilon)}}{2\beta(1 + h)}. \quad (14)$$

If the cost of eviction, ε, is 0, then Equation 14 is the same threshold for group stability as in the concessions-based model (see also Johnstone and Cant 1999). If $\varepsilon > 0$, groups may be stable even if $h \leq 0$.

When eviction is not costly (i.e., $\varepsilon = 0$), and males are of equal genetic quality ($y = 1$), the clutch size predictions of the restraint model are identical to those of the concessions model (Figures 1–3), even though the mechanisms determining reproductive division and group membership differ. Adding costs of eviction results in decreased $n_{\min}$ so that groups are more likely to be stable overall and also more likely to be stable at n_g^*. The effects of relative subordinate quality on model predictions are similar to those in the concessions-based model. Indeed, although the shape of the curve relating maximum clutch size and quality differs between the models (Figure 3a,b), these curves intersect the threshold for subordinate departure at the same value in both models. In other words, the threshold subordinate quality for group dissolution is the same in both models. The threshold quality at which females can produce their optimal clutch size is not the same in the 2 models. Although the intersection of n_g and $n_{\min}$ is not shown, by extrapolating these lines on Figure 3, it is apparent that this intersection occurs at a lower value of subordinate quality in the concessions model. In other words, females can produce their optimal clutch and still retain the subordinate at lower values of subordinate quality in a concessions-based system than in a restraint-based one. Another difference between the models is that if eviction is costly, $\varepsilon > 0$, and subordinates are of higher quality than dominants ($y > 1$), grouping can be stable in the restraint model, but not the concessions model, even if subordinates do not help (or are harmful to offspring survival, $h \leq 0$). We would expect a similar effect if subordinates increase female fitness by improving the genetic diversity of her offspring or allow females to bet hedge.

As in the previous model, the predicted proportion of direct reproduction obtained by the subordinate (p^*) depends on clutch size (Figure 4). When clutch size is at the female optimum, p^* shows the same patterns as in the classical restraint model (Johnstone and Cant 1999), that is, it decreases with increasing opportunities for independent breeding (at least when group members are related) and increases with increasing relatedness (Figure 4b). However, when clutch size is adjusted to retain subordinates in the group, p^* increases with increasing opportunities for independent breeding, the opposite pattern to that predicted by previous restraint models (Johnstone and Cant 1999) and is not influenced by relatedness (Figure 4b). Furthermore, p^* is the same as predicted in the concessions-based model (Figure 4a,b).

Tug-of-war model

In the tug-of-war model, group membership is not an issue. Rather, dominant and subordinate males compete in ways that reduce overall group productivity (e.g., by eating eggs or killing offspring). Investment in competition by dominants and subordinates, respectively, is denoted d and u. Subordinates are assumed to be less efficient at competition (b):

$$p = \frac{bu}{d + bu}. \quad (15)$$

The fitness functions for dominant and subordinate males and females, respectively, are

$$w_{\mathrm{D}}(n) = (n - u - d) s(n, d, u)[(1 - p) + rpy], \quad (16)$$

$$w_{\mathrm{S}}(n) = (n - u - d) s(n, d, u)[py + r(1 - p)], \quad (17)$$

$$w_f(n) = (n - u - d) s(n, d, u)[(1 - p) + py] + f_f(n), \quad (18)$$

where

$$s(n, d, u) = (1 - \beta(n - u - d)).$$

We solve for optimal values of n, u, and d, given the behavior of the other players in the system as in Reeve et al. (1998) (see also Johnstone 2000). Joint maximization of this system of equations generally could not be performed analytically, so we used numerical approximation in Maple 11.0 (Waterloo Maple Inc., Waterloo, Ontario, Canada). For a subset of models that could be solved analytically (i.e., $y = 1$), the second partial derivatives of these 3 fitness functions with respect to u, d, or n, respectively, at the equilibrium were negative; thus, this point represents a locally stable equilibrium. All model results were also confirmed with agent-based simulations incorporating replicator dynamics and occasional mutations to check for local stability (Hamilton IM, unpublished modeling results).

Clutch size is predicted to decrease with increasing relatedness between males and as subordinate quality declines (upper surface on Figure 5a). This effect is particularly strong when males are relatives (e.g., $r = 0.5$ on Figure 5a). Clutch size is also predicted to increase slightly as subordinate competitive ability increases when $r > 0$ (not shown). However, these trends refer only to clutch size produced. The number of surviving offspring increases with increasing relatedness between males (the lower surface on Figure 5a), so that a smaller proportion of offspring is lost (a parameter referred to as "aggression" in Johnstone 2000) when males are relatives. The proportion of the clutch lost increases as subordinate male quality increases.

For all of the parameter space explored, clutch sizes are larger and the numbers of surviving offspring are smaller than expected in the absence of male–male competition (i.e., when d and u are both 0). As an example, on Figure 5a, the expected clutch size in the absence of male–male competition when $y = 1$ is 50.0 with 37.5 surviving offspring.

The division of reproduction between males does not differ from that expected under the classical tug-of-war model when males are of equal genetic quality. The proportion of direct reproduction obtained by subordinates (p) increases with increasing subordinate efficiency, and there is little influence of relatedness except when subordinate efficiency is very poor

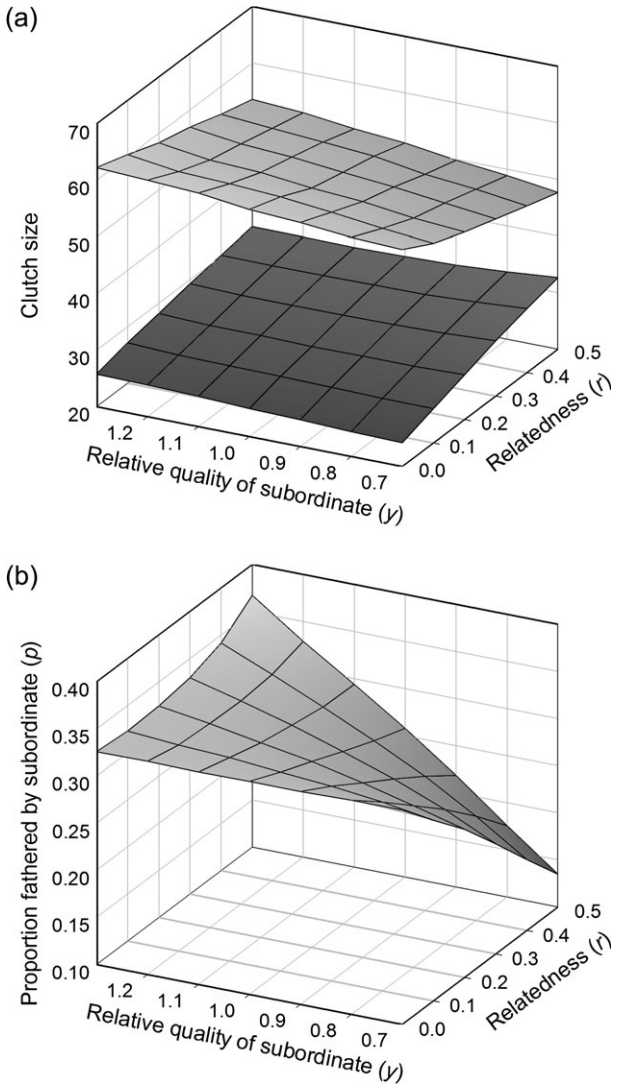

Figure 5
Effects of relative quality of subordinate males (y) and relatedness (r) on (a) predicted clutch size produced (upper surface) and surviving (lower surface) and (b) proportion of offspring of subordinate male in the tug-of-war model. For comparison, the expected clutch size in the absence of male–male competition in (a) when $y = 1$ is 50.0 with 37.5 surviving offspring. Other model parameters: $b = 0.25$, $\beta = 0.005$, $\alpha = 0.005$.

(see Reeve et al. 1998). However, if dominant and subordinate males differ greatly in quality, relatedness may have strong effects on the subordinate's share of direct reproduction (Figure 5b). This share should decrease with increasing relatedness if subordinates are of poorer quality than dominants but increase with increasing relatedness among males if subordinates are of higher quality than dominants.

DISCUSSION

These models predict that females may benefit from increasing their clutch size when there is a threat of subordinate male departure or when male–male competition is particularly costly. In the first of these cases, increases in clutch size are predicted to be greatest when opportunities for independent breeding are high (but not sufficiently high that grouping is unstable) and the effects of helping behavior of subordinate males on offspring survival are low but not negligible. As the effects of help increase or opportunities for independent breeding decrease, subordinates should be more willing to stay in the group and dominants should be more willing to accept subordinates. Females are therefore able to produce clutches closer to or at their own optimum size.

Female control over clutch size strongly influences the division of reproduction among males. The predictions of classical skew models are retained only when female clutch size is invariant. Indeed, in the case of the restraint framework, the predicted relationship between ecological factors and reproductive skew is the exact opposite of that predicted in the classical 2-player model. In both the concession and restraint models, relatedness, a key variable influencing skew in classical models, has no effect on reproductive division when female clutch size is superoptimal. Many experimental and observational tests of transactional skew models have focused on the predicted relationships between relatedness and skew (increasing skew with increasing relatedness in concessions models, decreasing skew with increasing relatedness in restraint models; e.g., Field et al. 1998; Ruppell et al. 2002; Langer et al. 2004; Nonacs et al. 2006; reviewed in Magrath and Heinsohn 2000; Reeve and Keller 2001). Few tests have found support for these predictions, suggesting that transactional models are of limited applicability. However, our models show that the lack of a relationship between relatedness and skew is not inconsistent with the transactional framework. The studies cited above focused primarily on skew among females (e.g., Field et al. 1998; Ruppell et al. 2002; Langer et al. 2004; Nonacs et al. 2006) and therefore cannot be directly compared with the predictions of this model; however, we emphasize that the decisions of other group members may lead to very different predictions than would be obtained from considering only dyadic interactions.

In the second class of models, the tug-of-war framework, subordinate departure is not a concern. However, competition between males to monopolize paternity leads to a reduction in group productivity. In this case, females are predicted to compensate partially for these losses by producing a larger clutch. Initial clutch size is always greater, and the number of offspring surviving is always lower when there are 2 competing males than when there is only one male in the tug-of-war model. Furthermore, initial clutch size is expected to be greatest when relatedness between dominant and subordinate is low and, if relatedness >0, when subordinate efficiency at converting investment in competition into competitive success is high. These conditions are likely to result in a high proportion of the clutch being lost to male–male competition. Surviving clutch size is also lowest for these values, indicating that compensation is not complete.

We found that relative quality of subordinates influenced model predictions. Females benefit from the presence of high-quality subordinates that father offspring and therefore are more willing to incur costs to retain these males. Clutch size declined with decreasing quality of subordinates in all models. This can be seen clearly in the tug-of-war model. However, this is also the case in the transactional models. On Figure 3, the clutch size necessary for retention of the subordinate is invariant with respect to subordinate male quality and represents a minimum clutch size in the group. If subordinates are of sufficiently high quality, females may benefit from producing a clutch larger than this. Thus, clutches with high-quality subordinates will be the same size or larger than those with poor-quality ones. Groups with low-quality subordinates may also disband.

In the restraint model, females may increase clutch size to retain subordinates that do not help raise offspring if subordinates are of sufficiently high genetic quality that the increase in current offspring quality offsets current and future

costs of clutch size and helper presence. The ability of females to increase clutch size results in groups being stable despite lack of subordinate help over a much broader range of parameter space than if clutch size were fixed. For example, in the classical restraint model, an unrelated subordinate that does not help but does steal reproduction can only steal, at maximum, ε units of reproduction. Grouping would then only be stable if $x < \varepsilon$. In the current model, the amount that it could steal is a function of the costs of producing young, opportunities for independent breeding and, to a much lesser extent, the cost of expulsion, and can range from 0 to 1 (in principle). Grouping can be stable over a wide range of parameter space as long as $y > 1$.

The models presented here are very simple and have the same drawbacks as other simple skew models. The models assume simultaneous decisions of all players and perfect knowledge of clutch size (discussed below), male quality, dispersal options, and the thresholds such as p^* and $n_{\min}$. They also assume that fitness payoffs are density independent. The incorporation of density-dependent fitness payoffs can have profound implications for the predictions of skew and similar models (Kokko and Sutherland 1998; Pen and Weissing 2000; Hamilton and Taborsky 2005). This is likely to be particularly relevant to the models presented here; females that produce large clutches may end up having large numbers of helpers competing for dominant position (although we do not consider resource inheritance in the current model). If all females in a population produce large clutches, this may increase competition for vacant territories, leading to higher constraints on dispersal and smaller clutch sizes.

These models assume that all individuals make decisions simultaneously. This assumption is also implicit in most other skew models (but see Hamilton 2004). Clearly, the sequence of decisions may have important implications for the expected equilibrium of these games. If, for example, dominant males decide to tolerate subordinates first, then subordinates may be able to parasitize and females produce a smaller, female-optimum clutch without the risk of immediate group dissolution. Incorporating the sequence of moves in the game would be a valuable addition to these and other skew models.

A critical assumption of the transactional models is that all group members have information regarding clutch size. We expect lack of information will strongly influence the model (as in Kokko 2003; Hamilton and Taborsky 2005). Consider an extreme case in which males have no information regarding clutch size except some population-level average. If males tolerate one another, but the population average clutch size exceeds the female's optimum, a female that produces a smaller clutch would initially do very well. As these "small-clutch" females spread in the population, males would receive insufficient direct reproduction to tolerate one another. A female that did produce a larger clutch again would gain no benefit because males would not have information that the clutch is larger. Thus, we would expect the system to degenerate into pair breeding.

Do males have information regarding clutch size? This would seem to depend on the mechanisms of fertilization and the timing of egg laying. With viviparity, long-term sperm storage or other delays between copulation and offspring production, such information will not be available immediately, if at all. Indeed, with internal fertilization in general, we would expect females often (but not necessarily) to have more control over the division of reproduction than is assumed in the model. Similarly, unless both males are able to inspect the clutch after it is laid, the required information about clutch size will not be available to one or both males. Thus, we expect this model to be most applicable to external fertilizers (particularly those in which sneak spawning occurs) in which all males perform direct brood care (and have the opportunity to measure brood size), as in certain cooperatively breeding fish (e.g., *N. pulcher*, Taborsky 1984; *Neolamprologus multifasciatus*, Kohler 1998; *Neolamprologus savoryi*, Heg et al. 2005; *Julidochromis ornatus*, Awata et al. 2005; Heg and Bachar 2006).

Although few systems may meet all the assumptions of these models as written, the general predictions are applicable to a wider range of breeding groups. The restraint model presented here is also consistent with a model of full female control over the distribution of paternity but with dominant males having control over group membership (Hamilton IM, unpublished modeling results). Again, this version of the model assumes simultaneous decisions of females and dominant males and that the dominant males have complete information regarding the division of paternity.

Our models illustrate how strategic decisions by females over parental investment and mate choice and by males over group membership and investment in competition interact to influence reproductive division and group stability. They make testable predictions regarding the influence of within-group conflict over group membership or group productivity on clutch size. Although the variables influencing this conflict may differ (opportunities for independent breeding in transactional models, cost of expulsion in restraint models, relatedness, and subordinate quality in tug-of-war models), all 3 models predict that increased likelihood of group dissolution or within-group aggression result in larger clutches, at least initially. There is some existing support for this prediction. In the cooperatively breeding cichlid, *N. pulcher*, breeding females increase their clutch size when helpers have the opportunity to disperse (i.e., x is high) when helpers are male but not when helpers are female (Heg et al. 2006). It is not clear whether the assumptions of these models are met in this system, although, in general, tug-of-war or restraint models best describe the system (Heg et al. 2006).

The models also have important implications for existing and future tests of the transactional and tug-of-war hypotheses. Over a wide range of parameters, relatedness has no influence on skew in the transactional models presented here but may influence skew in tug-of-war models (when male qualities differ). These are opposite of the commonly tested predictions of the classical models. However, our models do make several predictions by which the 2 hypotheses may be distinguished, if females can adjust clutch sizes. The tug-of-war model predicts that clutch size decreases with increasing relatedness between males; the transactional models predict no such relationship. The tug-of-war models also predict an inverse relationship between initial clutch size and final or surviving clutch size. Thus, initial clutch size increases and surviving clutch size decreases with decreasing relatedness and increasing subordinate quality. In the transactional models, increases in initial clutch size are associated with equal or greater numbers of surviving offspring whenever breeding with 2 males is stable (although, by definition, a smaller proportion survives if $\beta > 0$).

Finally, our models highlight the influence that other group members may have on the outcome of dominant–subordinate interactions in general (see also Reeve 1998; Cant and Reeve 2002; Hamilton and Dill 2002; Frank 2003; Wenseleers et al. 2004). Direct intervention in conflicts by third parties is frequently observed in many social systems (e.g., insects: Ratnieks 1988; Monnin and Ratnieks 2001; fish: Walter and Trillmich 1994; Schradin and Lamprecht 2000; primates: Flack et al. 2005) and may be a critical component of conflict reduction in animal societies (Frank 1995, 2003). Indirect intervention as considered here may be similarly important. Our models also demonstrate the importance of the interaction between mate choice and intrasexual conflict on the reproductive success of

group members (as in, e.g., female willingness to increase clutch size to prevent high-quality subordinates from leaving or being evicted). Previous considerations of this interaction have generally focused on female incitement of male–male competition (Wiley and Poston 1996); here, we show a potential role for female mate-choice decisions in alleviating conflict as well.

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