# Predicting polygynous settlement while incorporating varying female competitive strength

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The rationale behind the polygyny threshold model is that the breeding situation quality (BSQ) males have to offer females varies, and that differences in BSQ offset females' costs of sharing with other females, thus favoring polygynous settling. It predicts that the first chosen territories become polygynous first, and that breeding success of secondary and contemporary monogamous females is similar. This is not generally found. Testing of the polygyny threshold model (PTM) assumes that females are equal competitors and distribute ideally free around available breeding resources, a condition probably not often met. If sharing a male is costly, and competitors differ in quality, weaker individuals should experience degrees of competitive exclusion. Setting female competitive abilities proportional to arrival order, we use an individual-based interference-competition model to examine settlement patterns. Shifts in the ratio of variance in interfemale competitiveness to interterritorial differences in BSQ result in various settlement patterns, with different predictions concerning settlement order and fitness returns. We find support for the novel predictions from data on northern lapwing (*Vanellus vanellus*), starling (*Sturnus vulgaris*), pied flycatcher (*Ficedula hypoleuca*), and blue tit (*Parus caeruleus*). We suggest that before testing polygyny predictions, an evaluation of the settlement sequence should be made, which may help to generate more accurate predictions. We argue that violation of the "equal female" assumption may explain much of the discrepancy between predictions and empirical findings in previous tests of the PTM, and that secondary females in general have lower success than do monogamous breeders because they are of lower quality. *Key words:* competition, cost-compensation, mating system, polygyny, settlement order, social dominance. *[Behav Ecol 14:257–267 (2003)]*

$S$ince the mid 1960s when the polygyny threshold model (PTM) was proposed (Orians, 1969; Verner, 1964; Verner and Willson, 1969), a large bulk of empirical studies have been undertaken to test its validity and predictions (for review, see Slagsvold and Lifjeld, 1994; Webster, 1991).

The PTM describes settlement in resource based polygynous systems. Variance in the breeding situation quality (BSQ) that the males offer, that is, differences in the total breeding resources offered to the females by individual males (Wittenberger, 1976), may lead to the situation in which a prospecting female prefers to settle as secondary female on a territory already colonized by a female, rather than choosing monogamous status by settling on a vacant territory. She is predicted to do so if, after subtracting component costs (sensu Bensch, 1997) of sharing a territory with another female, the BSQ of the best territory is still higher than that of the best bachelor territory.

The PTM predicts the following: (1) secondary females should have similar fitness returns to those of contemporary monogamous breeders (Alatalo et al., 1981; Garson et al., 1981), and (2) the most attractive territories (the first territories to be settled) should reach polygynous status first, resulting in a positive correlation between territory quality and harem size, and between settling order of primary and secondary females (Altmann et al., 1977; Davies, 1989; and references therein). From this, primary females on polygynous territories should settle earlier than monogamous females.

The model rests on the following assumptions: (1) there is variation in BSQ, (2) females can accurately assess BSQ of the males breeding in the system, (3) females value BSQ in a similar manner, (4) females prefer breeding territories with the highest BSQ, (5) females experience costs of sharing a mate, (6) females are of equal quality and distribute themselves on offered BSQ in an ideally free fashion, and (7) the operational sex ratio is not skewed toward a surplus of breeding females.

Studies reviewing tests of the PTM (Slagsvold and Lifjeld, 1994; Webster, 1991) conclude that empirical evidence does not support its predictions. Generally, monogamous females are found to have higher breeding success than that of secondary females. Also, in some studies, the earliest settled territories (presumably of highest BSQ) often remain monogamous instead of becoming polygynous (Pinxten and Eens, 1990; Smith et al., 1994; Wootton et al., 1986; this study). Studies that have tested the predictions have proffered several explanations for the observed discrepancies. These include no or low costs of polygyny (Searcy and Yasukawa, 1995; Wootton et al., 1986), sexy son effects (Weatherhead and Robertson, 1979), a female-biased sex ratio (Searcy and Yasukawa, 1989), maladaptive choice/female mate sampling bias owing to high search cost (Searcy and Yasukawa, 1989; Stenmark et al., 1988), unpredictable environment (Wittenberger, 1981), deception (Alatalo et al., 1981), and systematic differences in quality of females of different mating status (Davies, 1986; Forstmeier et al., 2001a,b; Lenington, 1983; Simmons et al., 1986; Webster, 1991; Wittenberger, 1981).

Common for studies modeling cost-compensation polygyny (the PTM and modified versions; see Altmann et al., 1977; Bensch and Hasselquist, 1991; Garson et al., 1981; Leonard,

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1990; Slagsvold and Lifjeld, 1994; Weatherhead and Robertson, 1979) is the underlying assumption that all females are inherently considered of equal quality and differ only in the strategic decisions they make in relation to the extrinsic environmental influences to which they are subjected. In most systems, it seems unrealistic not to expect variation in female quality. Competitive abilities and prospects of reproductive output are likely to vary, reflecting maternal differences in age and/or genetic variation in traits that affect reproductive performance (e.g., condition, competitive skills, and breeding experience; Forslund and Pärt, 1995, and references therein). Davies (1986) observed at least seven nest desertions that were the direct result of aggression between female dunnocks (*Prunella modularis*), and Davies and Houston (1986) stressed in an accompanying study that "there is a more general reason for why the [polygyny threshold] model is likely to fail in predicting observed mating systems—namely, it largely ignores conflicts of interests between individuals." Sandell (1998) showed experimentally that aggression level of female starlings (*Sturnus vulgaris*) varied between individuals, and that aggressive females were more likely to end up as monogamous breeders than less aggressive females.

If we accept that there is often individual variation in female competitive ability, it is important to determine the distribution of these differences in relation to mating status before formulating predictions. Differences in the competitive abilities of interacting females are likely to lead to asymmetry in interference costs, with the stronger female monopolizing a larger proportion of the limited resource. The degree of difference in the division of breeding resources between territories may therefore be determined by the difference in competitive ability of interacting polygynous females. Our view is that incorporating female despotic ability has great potential in explaining the observed discrepancy concerning predictions in systems in which sharing costs have been documented. Questioning the general validity of the equal-female assumption, we offer an alternative framework for predicting settlement patterns using a model that accommodates interfemale differences in competitive strength. This gives predictions regarding fitness returns and the settlement order of females that sometimes differ from the PTM. It is also applicable for polygynous systems in which the sex ratio is skewed toward a surplus of females. We use this approach to evaluate polygyny in northern lapwings (*Vanellus vanellus*), European starlings, pied flycatchers (*Ficedula hypoleuca*), and blue tits (*Parus caeruleus*).

## Evaluation of assumptions

Including variable female competitive ability requires fulfillment of the following assumptions in addition to assumptions 2, 3, and 4 of the PTM listed in the Introduction:

### Assumption 1. Females differ to a variable extent in competitive abilities
Several studies have documented variation in competitive abilities and the existence of dominance relationships (Piper, 1997; Sutherland, 1996; and references therein), and specifically for polygynous females during breeding (see Arcese, 1989a,b; Langston et al., 1990; Roberts and Searcy, 1988; Simmons et al., 1986; Slagsvold and Lifjeld, 1994; and references therein).

### Assumption 2. Females can assess the competitive strength of female antagonists in relation to their own
This information may be gathered from challenges and contests or through assessments of quality-indicating traits. When dominance interactions exist and play an important

role in regulating access to resources in a social system, the interactors may benefit greatly if they can establish the likely outcome of a contest without fighting, and instead use mutual assessment to determine the dominance relationship. Measuring behavior and the displaying of characters that are honest signals of condition and strength are common in social systems in which ownership of economically defendable resources (sensu Emlen and Oring, 1977) are subject to contests (Krebs and Davies, 1993).

### Assumption 3. Females benefit from nesting as early as their condition permits
A large number of studies of a variety of bird species have showed that reproductive output in general declines seasonally (see Daan et al., 1988; Drent and Daan, 1980; Langston et al., 1990; Perrins, 1970). This relationship may emerge (1) from a strategic decision motivated by a seasonal decline in reproductive value of offspring, (2) because seasonally deteriorating extrinsic breeding conditions may impose increasingly large costs to an individuals' condition or survival, or (3) because breeders arriving late are intrinsically less resourceful than early breeders (see Daan et al., 1988; Drent and Daan, 1980; Perrins, 1970). Because there are obvious costs associated with early breeding (e.g., rough weather conditions and sparse food) it is likely that individuals of high condition—which are best able to withstand adverse conditions—migrate earliest, arrive first at the breeding site, and have the advantage of choosing breeding territory first. The evolutionary stable strategy would then seem to be a condition dependent decision as to when to start breeding (Daan et al., 1988; Drent and Daan, 1980). If competitive ability is condition-dependent, a further assumption may be justified:

### Assumption 4. If present, differences in competitive abilities decrease from first to last settled female
Dominance interactions occur in most bird species, and dominance relationships are typically consistent between different social contexts and of a linear nature (Piper, 1997). In the well-studied polygynous red-winged blackbird (*Agelaius phoeniceus*), female dominance varies and is strongly related to the order of female settlement and to female size (Cristol, 1995; Langston et al., 1990; Roberts and Searcy, 1988). In pied flycatchers, females with the longest residency were most likely to win contests over nest sites and mates (Dale and Slagsvold, 1995). Similarly, in male and female dark-eyed juncos (*Junco hymalis*), dominance was related to prior residency (Cristol et al., 1990).

### Assumption 5. Strong females monopolize resources at the cost of weaker females to a degree determined by the relative difference in competitive abilities of the female antagonists
If competitive interactions occur and competitive ability is condition-dependent, it is likely that resources are distributed among contestants in a ratio proportional to the difference in competitive strength of contestants (Davies, 1986; Goss-Custard, 1988; Kempenaers, 1995; Roberts and Searcy, 1988; Sandell, 1998; Sutherland, 1996).

## Framework and model

We model a system in which 15 prospecting females are sequentially introduced to a breeding site where 10 males maintain breeding territories. The strongest female is allowed to arrive and choose a mate first, and subsequent females are introduced according to rank. Each female assesses the quality $Q_i$ of all territories $i = 1, \ldots, 10$ before making her choice.

The best territory $Q_1$ is assigned the arbitrary value 1, and territory quality decreases with the factor $q^{i-1}$, $i = 1, \ldots, 10$, $q [0,1]$:

$$Q_1 = Q_1 q^{i-1}. \tag{1}$$

A decrease in the value of $q$ increases the difference in BSQ between territories. The level of difference in competitive strength between the settling females $n = 1, \ldots, 15$ is similarly generated by setting the arrival order proportional to competitive strength $C_n$. The first female $C_1$ is assigned the competitive strength of one, and competitiveness of subsequent settlers decreases by the factor $c^{n-1}$, $n = 1, \ldots, 15$, $q [0,1]$. Individual competitive rank is then described by:

$$C_n = C_1 c^{n-1}. \tag{2}$$

By varying the value of $c$, the difference in competitive strength is varied in the same manner as $q$, and by varying the values of $q$ and $c$ relative to one another, the ratio of the differences between territories and females is varied. A number of different distributions of female quality and BSQ can easily be implemented in the model.

We proceed to sequentially estimate optimal choices for the individual female settlers. We let individual sharing costs depend on the relative differences in competitive strength between interacting females, such that female $n$ obtains a fraction $R_i(n)$ of the BSQ corresponding to her fraction of competitive strength:

$$R_i(n) = \frac{C_n}{C_n + \sum_{j=1,15} C_i p_i(j)}, \tag{3}$$

where $p_i(j)$ indicates the presence ($p = 1$) or absence ($p = 0$) of female $j$ in territory $i$ at the time female $n$ makes her decision. This fraction results in stronger females monopolizing a greater proportion of the available breeding resources than weaker females. On arrival, each female evaluates all territories and settles on the territory $i^*$ that maximizes $W(n)$, that is, the territory offering the highest payoff after subtracting sharing costs incurred by resident female antagonists.

$$W_{i^*} = \max_i [Q_i R_i(n)] \tag{4}$$

Here, $W_{i^*}(n)$ denotes the payoff on the territory (of the 10 sampled territories) that gives the maximum payoff for the settling female $n$, and $Q_i$ equals the payoff for a territory $i$ that a female would get were she alone on that territory.

## Simulation results

By using this procedure, we simulated six settlement scenarios. We were interested in the effect of varying female competitive strength on a system with a certain variance in BSQ, so we set $q = 0.905$ for all scenarios and conducted six runs with different values of $c$, ranging from identical females to large differences between females (Figures 1a–f). We chose a value of $q$ of 0.905 for convenience, because during trials, a lower value resulted in trigamous territories in scenarios with $c = 1$ (equal females). Different values of $c$ were chosen to visualize examples of different settlement patterns.

### Scenario a. Females are equal competitors, no seasonal decline in reproductive success
In Figure 1a, the settlement is identical to settlement observed under the classical PTM with females of equal quality. In this scenario, early colonized territories become polygynous first, and primary females settle before monogamous females do. Monogamous and secondary territories are more or less
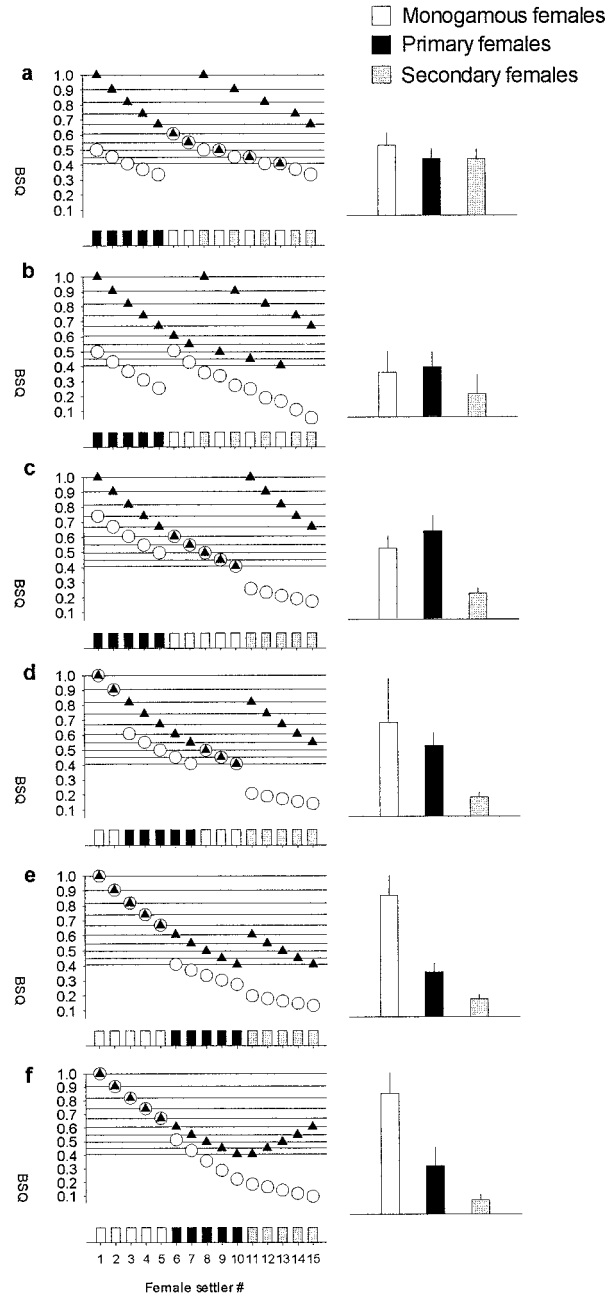


**Figure 1**
This figure shows six different scenarios of polygynous settlement in which female competitiveness, denoted by $c$ (from Equation 3), is varied through scenario a–f from identical females (scenarios a and b, $c = 1$), via small difference (scenario c, $c = 0.90$, or 10%), intermediate difference (scenario d, $c = 0.875$, or 12.5%) to larger differences between females (scenario e, $c = 0.865$, or 13.5%; scenario f, $c = 0.83$, or 17% ). Females are introduced sequentially to the system from female settlers 1 through 15. Values of the y-axis describe BSQ of the 10 territories in the system. Horizontal lines indicate the BSQ of each territory, and triangles denote the initial BSQ of the preferred territory for each female settler. In all four scenarios, the factor determining the difference between territories ($q$) is set to 0.905. Circles represent the actual proportion of BSQ that each female enjoys after subtracting sharing costs. In monogamous relationships, this is equal to the BSQ of the territory. Bars indicate mean amount of BSQ that females of different mating status acquire, and make use of the same y-axes as the settlement figures (white bars denote monogamous females; black bars, primary females; and grey bars, secondary females). Error bars signify 1 SD.

evenly interspersed over the settlement sequence. In this case, primary and secondary females on the same territory each receive 50% of the available BSQ resources and have therefore equal fitness. Monogamous females have a slightly higher success than do polygynous females, because the BSQ of some of the territories they occupy is higher than the fitness enjoyed by polygynous females on the high-quality territories. This scenario with polygynous females dividing the available BSQ equally between themselves is identical to that described by Davies (1989: Figure 2, case b, scenario 2). In this scenario, there is no seasonal decline in reproductive success, and a positive correlation between settlement order of primary and secondary females exists.

### Scenario b. Females are equal competitors, seasonal decline in reproductive success

In this case, the success of primary females relative to monogamous and secondary females depends on the slope of seasonal decline in reproductive success. The steeper the slope, the relatively higher the reproductive advantage enjoyed by primary females. If $Q$ is reduced by 2% (arbitrarily chosen) between each consecutive female in the sequence, primary females as a group exhibit the highest success, and secondary females the lowest (Figure 1b). There is a positive correlation between settlement order of primary and secondary females.

Because a seasonal decline in reproductive success is commonly observed, it has been proposed that restricting analyses to comparisons of contemporary monogamous and secondary females is a more correct test of the PTM. As monogamous and secondary females are evenly distributed in the sequence from settler 7–14 (Figure 1a,b), it appears that if a seasonal decline in reproductive success is present, comparisons of monogamous and contemporary secondary females over this stage of the sequence should constitute a sound test of the settlement model.

### Scenario c. Female competitors differ (10%)

In Figure 1c, an interfemale difference in competitive strength is set to 10% ($c = 0.90$). A seasonal decline is introduced by letting early females have a higher competitive quality; that is, the seasonal decline is owing to intrinsic, not extrinsic, aspects of the system. Early settled territories achieve polygynous status first; primary females precede monogamous females in the sequence; and females of different mating status segregate in defined groups. Primary females have slightly higher fitness returns than monogamous females, and they both have higher fitness than secondary females. There is a positive correlation between settlement order of primary and secondary females.

### Scenario d. Female competitors differ (12.5%)

In Figure 1d, interfemale difference in competitive strength is increased further to 12.5% ($c = 0.875$). Here some of the monogamous females gain their status through successful deterrence of subsequent prospectors. First colonized territories no longer become polygynous, and fitness returns decrease from highest success in monogamous females, via a slightly lower success in primary females, to lowest success in secondary females. There is a positive correlation between settlement order of primary and secondary females.

### Scenario e. Female competitors differ (13.5%)

In Figure 1e, interfemale difference in competitive strength is increased again to 13.5% ($c = 0.865$). All the monogamous territories have a higher initial BSQ than that of the polygynous territories, monogamous females gain their status

through successful deterrence of subsequent settlers. Monogamous females get the highest fitness, followed by primary females, with secondary females exhibiting the lowest fitness. There is a positive correlation between settlement order of primary and secondary females.

### Scenario f. Female competitors differ (17%)

Finally, in Figure 1f, interfemale difference in competitive strength is set to 17% ($c = 0.83$). Monogamous females settle first and occupy the territories of highest quality, achieving their status by deterring subsequent prospective settlers. Monogamous females are predicted to have highest success; primary females, intermediate success; and secondary females, the lowest success. There is a negative correlation between settlement order of primary and secondary females. Increasing $c$ further leads to an increased incidence of monogamy; that is, that some females are forced to forego breeding.

See Table 1 for a summary of scenarios and predictions. Similar scenarios can be produced with different levels of $q$ and $c$. What, in essence, determines the settlement results is the ratio between $q$ and $c$. A large $c$ relative to $q$ (equal females versus differing BSQ) gives results that are consistent with ideal free distribution expectations. A small $c$ relative to $q$ (differing females versus equal BSQ) describes a system in which female despotism is the most important factor in determining the settlement result.

### Predictions

With increasing difference in competitive ability among females in relation to the differences among territories in BSQ, settling order of monogamous females should be skewed to earlier settlement relative to primary and secondary females. This should also be reflected in reproductive success; the relative success following the order of settlement. Monogamous females that breed at the same time as primary females should have similar or higher reproductive success than primary females. The exact difference would depend on the rate at which competitive abilities decline with settling order, since this dictates the sharing rules between primary and secondary females. To be more specific, in systems in which female competition is sufficiently low:

- All primary females should precede monogamous females in the settling order.
- Secondary females should start to settle on the territories of highest BSQ, so that first settled territories end up polygynous, resulting in a positive correlation between BSQ and harem size.

In systems in which female competition is notable:

- Monogamous females should settle relatively earlier; in systems with high levels of competition, they settle before or at the same time as primary females.
- In systems with moderate to high levels of female competition, monogamous status may result from early settlement and successful monopolization of breeding resources, or from late settling on a low quality territory. In such a system, there should be a larger variance in quality and settling date in monogamous females than in primary and secondary females.
- Secondary females start to settle on territories of intermediate or low BSQ, so that there is no positive correlation between BSQ and harem size.
- Monogamous females should have higher reproductive success than that of primary females, and primary females higher reproductive success than that of secondary females.
- With particularly high levels of competition, a negative correlation between settling rank order of primary and secondary females should arise.

**Table 1**

**Predictions derived from the model pertaining to reproductive success and settlement order**

| Estimated parameter | Scenario a ($c = 1$) | Scenario b ($c = 1$)[a] | Scenario c ($c = 0.90$) | Scenario d ($c = 0.875$) | Scenario e ($c = 0.865$) | Scenario f ($c = 0.83$) |
|---|---|---|---|---|---|---|
| Female reproductive success | M > P = S | **P ≥ M > S** | **P ≥ M > S** | **M ≥ P > S** | M > P > S | M > P > S |
| Variance in settling date | M = S > P | M = S > P | M = P = S | **M > P = S** | M = P = S | M = P = S |
| All (or most) monogamous females settle after primary females? | Yes | Yes | Yes | **No** | **No** | **No** |
| Positive correlation between BSQ and harem size? | Yes | Yes | Yes | **No** | **No** | **No** |
| Correlation between settlement order of primary and secondary female? | **Positive** | **Positive** | **Positive** | **Positive** | **Positive** | Negative |
| BSQ (or colonization rank) of the territory where the first secondary female settle | Highest | Highest | Highest | **Intermediate** | **Intermediate** | Lowest |

Summary of results from settlement simulations by using different values for variation in female competitive quality $c$. A decreasing $c$ indicates an increased steepness of the gradient in female competitive quality. The 10 territories decrease in BSQ with 9.5% ($q = 0.905$) between each territory from best (1.0) to worst (0.407) in all scenarios. Bold typefaces indicate the scenarios that best fit results found in the northern lapwing. Overall, scenario d was the scenario that matched best the results found in the lapwing.

M indicates monogamous females; P, primary females; and S, secondary females

[a] 2% decrease in value of $Q$ between each settling female in simulation of extrinsically decreasing seasonal breeding conditions.

- In all scenarios, secondary females as a group should have lower reproductive success than do monogamous females; if contemporarily breeding monogamous and secondary breeders are present, these should on average have similar success.

Cross-species comparisons should show that in systems in which females act aggressively towards one another:

- Monogamous females should on average settle relatively earlier than in systems in which females do not act aggressively toward one another.
- Differences in reproductive success between monogamous and primary females in polygynous (or facultatively polygynous) species should correlate with the degree of interfemale competition; in species with high levels of competition, success of monogamous females should be similar to or higher than that of primary females, and with low levels of competition, reproductive success of monogamous females should be lower than primary females' and more similar to that of secondary females.

**Empirical support**

A settlement pattern that is affected by varying female competitive abilities demands that the sharing of a male incurs costs. Otherwise there would be no motivation to compete. Thus, when searching for suitable systems for this model, we focused on systems where such costs have been documented. We used data from the northern lapwing (Byrkjedal et al., 1997; Grønstøl, 1997, 2001, 2003) to evaluate six predictions derived from the model (Table 1). In addition we used data on the European starling (*Sturnus vulgaris*; Pinxten and Eens, 1990; Smith et al., 1994), the pied flycatcher (Stenmark et al., 1988), and the blue tit (Kempenaers, 1994) to test predictions regarding reproductive output and timing of breeding of monogamous females relative to primary females. Polygyny is reasonably common in all these four species, and female aggression and attempts (sometimes successful) at evicting other prospecting females are well known (Grønstøl, 2001, 2003; Kempenaers, 1995; Liker and Székely, 1997; Sandell, 1998; Slagsvold et al., 1992). In these species, polygynous

settlement does incur costs of sharing a mate (Grønstøl, 2001, 2003; Pinxten et al., 1993; Pinxten and Eens, 1994; Kempenaers, 1995; Lifjeld and Slagsvold, 1990; Sandell et al., 1996; Smith, 1995). In the following, laying dates or nest initiation dates are used as estimates of the beginning of female breeding (nest start). The beginning of female breeding for each season was standardized in relation to date of first nest, and data were then pooled over the seasons.

*The northern lapwing*
Lapwing breeding data came from two sites in western Norway studied in 1991–1996 and 1998–1999 (Byrkjedal et al., 1997; Grønstøl, 1997, 2001, 2003). Primary and secondary status were assigned from the day of clutch completion. In lapwings, laying dates correlate significantly with arrival date (linear regression: $y = 0.49x + 13.60$, $n = 33$, $r^2 = .48$, $p < .001$). In seven cases, polygynous females on the same territory completed their clutch on the same day, so in these cases, primary and secondary status were assigned based on arrival dates. Figure 2a shows the cumulative distribution in clutch completion for female lapwings of different mating status. Monogamous females started breeding soon after the primary females (no significant difference in mean date of nest initiation), and secondary females followed significantly later than both primary and monogamous females. The fraction of monogamous breeders that laid before the last primary settler was high (84%; Figure 3a). Figure 3b shows the temporal distribution of these early monogamous females in relation to nest start of primary females. The estimates of spread (SD and 95% confidence limits) show that the high proportion observed in Figure 3a does not result from one of the primary females breeding uncharacteristically late, but that they actually do breed simultaneously. This overlap seems too large to be solely ascribed to imprecision in female choice when settling. These findings are contrary to the PTM-prediction that all primary females should settle before monogamous females, and matches well with scenario d (Figure 1).

Chick production data was available for the 1998 season (Hafsmo JE, personal communication). Figure 3c describes

**Figure 2**
Monogamous females nested earlier in the settlement order than is predicted from the PTM. The plots show cumulative percentage distributions of timing of breeding of females of different mating status (white circles denote monogamous females; black circles, primary females, and grey, secondary females) for (a) northern lapwings (seasons 1991–1996, 1998–1999), (b) starlings* (season 1991; from Smith et al., 1994), (c) starlings** (seasons 1984–1987; from Pinxten and Eens, 1990), (d) pied flycatchers (seasons 1985–1986; from Stenmark et al., 1988), and (e) blue tit (seasons 1990–1992; from Kempenaers, 1994). Estimates of initiation of nesting were standardized in relation to earliest nest in each season before pooling over seasons within species. Data for all species but the lapwings were read from diagrams. *P* values of paired comparisons are from Tukey post-hoc tests performed after significant results of one-way ANOVA with female mating status as grouping variable.
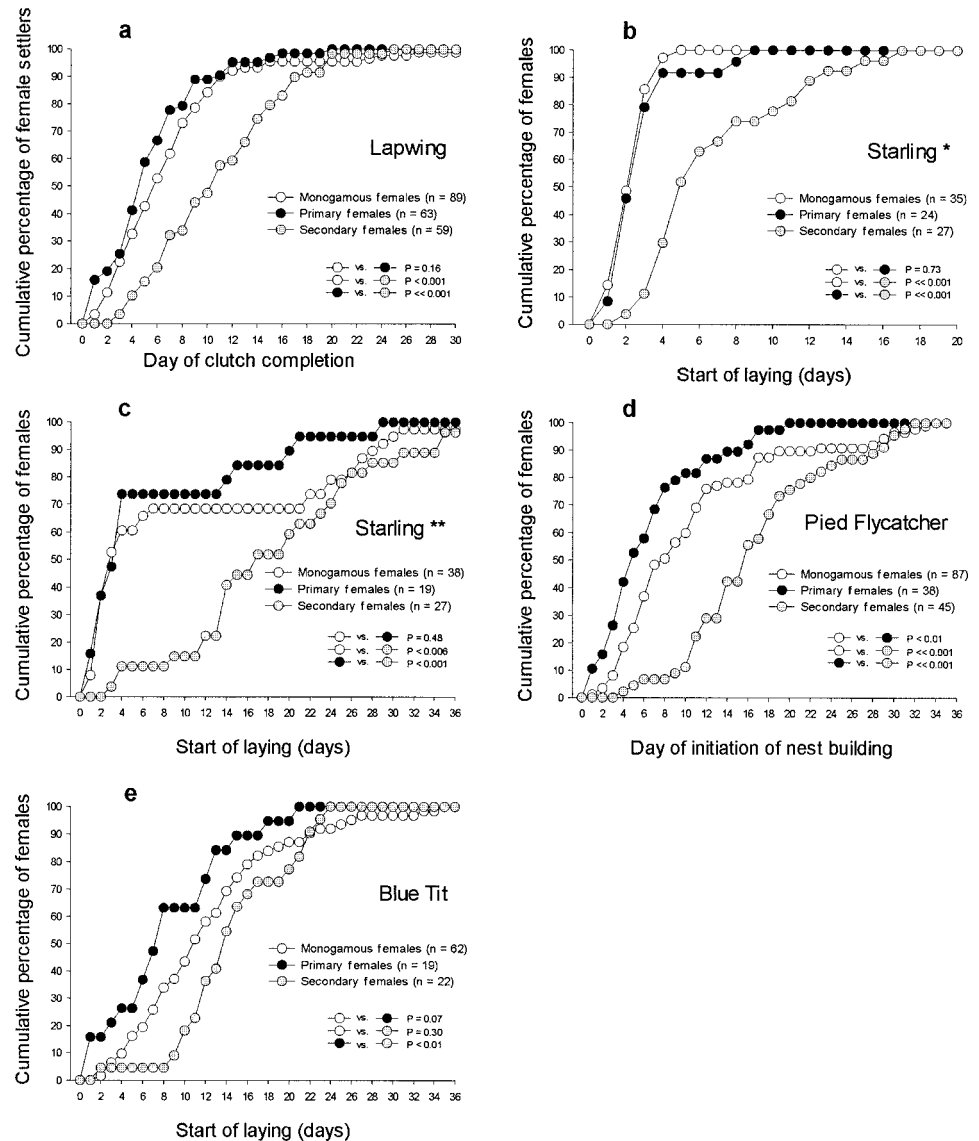
chick production at day 16 after hatching. This should constitute a reasonably good fitness estimate because the chick mortality rate levels out after the age of 2 weeks with very low mortality from 16 days of age (Blomqvist et al., 1997; Galbraith, 1988). Chick production estimates differed significantly among females of different mating status (ANOVA: $F_{2,25} = 3.93$, $p = .03$). Chick production of monogamous and primary females was similar, and both were higher than in secondary females. This fits well with fitness predictions expected from scenario d (Figure 1).

The variance in time of breeding start was highest in monogamous female lapwings, which is expected if monogamous females show a larger range in quality than primary and secondary females do as hypothesized in scenario d ($s^2$: monogamous females, 43.22, $n = 89$; primary females, 15.14, $n = 63$; and secondary females, 26.32, $n = 59$. $F$ tests (two-tailed): monogamous females versus primary females, $p < .001$; primary females versus secondary females $p = 0.03$; and monogamous females vs. secondary females, $p = .04$). The higher variance in settling dates of monogamous than primary females fits with predictions of scenarios a, b, and d. From scenarios a and b, secondary females should have

a variance similar to monogamous females, and from scenario d, it should be similar to that of primary females. The observed intermediate variance of secondary females does not match any of the scenarios perfectly, but considering that monogamous females bred as early as they did, scenario d is probably the best match.

Scenario d (Figure 1) also predicts no positive correlation between BSQ and harem size. Using the day of clutch completion of the earliest female on the territory as an estimate of BSQ, and relating this to harem size, produced no significant correlation, although there was suggestion of a trend (Figure 4a).

From scenarios a through e, there should be a positive correlation between settlement order of primary and secondary females on the same territory. Figure 4b show the correlation of the rank order of time of clutch completion of primary females and secondary females. The correlation was significant, although some residual variance was observed. Interestingly, there seemed to be a cluster of values in the upper left area of the graph. Scenario f predicts a larger interval between primary and secondary females on early colonized territories than on later colonized territories, so this

cluster may be the result of some females settling according to competitive differences in the range specified in scenario f.

Figure 4c shows the intervals in days between primary and secondary breeding in relation to timing of clutch completion of primary females. The mean (and maximum) interval values were larger and showed a large degree of variance early in the season. These values decreased with later breeding start of primary females. One would expect such a decrease if prospects of successful breeding diminished steeply after a certain date. Figure 4b suggests that such a temporal breeding threshold occurred roughly 20 days after breeding start of first breeding female.

The PTM predicts that secondary females should start colonizing the most attractive territory. Using time of clutch completion of first clutch on territory as an indirect indicator of BSQ, we examined the colonization rank order of the territory that first became polygynous for each of the eight separate seasons. The mean rank was 5.38 (SD, 3.89; $n = 8$). The mean number of territories each year was 19.5 (SD, 6.65; $n = 8$). The mean rank was significantly different from one (which is the null expectation that first colonized territory became polygynous first); one sample $t$ test: $t = 3.18$, df = 7, $p = .015$. These findings correspond to predictions posed by scenarios d and e.

### The European starling

Starling data stem from two studies, one made in two nest-box colonies in Antwerp, Belgium, during the seasons 1984–1987 (Pinxten and Eens, 1990), and one in seven nest-box colonies in southern Sweden during the 1991 season (Smith et al., 1994). Figure 2b,c shows that monogamous females nested relatively early in both studies. In the Swedish starling study (Smith et al., 1994), monogamous females, on average, nested even earlier than primary females, and both primary and monogamous females nested significantly earlier than did secondary females. This might suggest that the system is situated somewhere between scenarios d and f (Figure 1). In Sweden, all monogamous females nested before the latest primary breeder (Figures 2b and 3a,b), indicating that most of the females gained their monogamous status by successfully monopolizing breeding resources. This conforms well to scenario e or f. In Belgium, monogamous females also in general bred early (Figures 2c and 3a,b). As in the lapwings, monogamous starlings had the highest chick survival, significantly higher than that of secondary females. Fledging success of primary females was not significantly higher than that of secondary females (Figure 3c; Pinxten and Eens, 1990; Smith et al., 1994). We conclude that settling order data refute PTM-predictions, and the observed patterns of settling and fledging success were most similar to predictions of scenarios d and e.

### The pied flycatcher

We used breeding data on pied flycatcher from Stenmark et al. (1988), who studied flycatchers in three nest-box populations near Oslo, Norway, during the seasons 1985–1986. Primary females nested significantly earlier than did monogamous females, who again nested significantly earlier than secondary females (Figure 2d). However, a large fraction of monogamous females (90%) bred at the same time as primary females (Figure 3a,b), which conflicts with PTM predictions. The settlement order might suggest that the system conformed to scenario d or perhaps to somewhere between scenarios c and d. This was also supported by the fledging success pattern, in that fledging success of monogamous and primary females were in the same range, and both
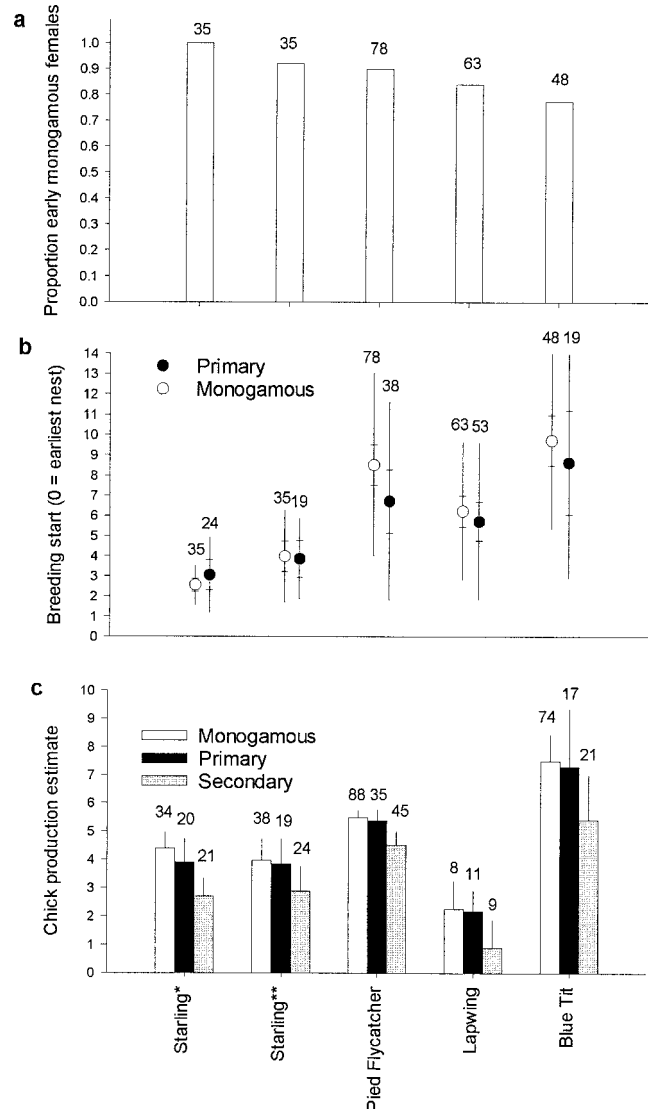


**Figure 3**
(a) The proportion of monogamous females that breed at the same time as primary females was high in lapwings, starlings, pied flycatchers, and blue tits. The bars describe the proportion of monogamous females that laid their nests before the latest primary female. Figures indicate sample sizes of early monogamous nests (defined as number of monogamous nests laid earlier in the laying order than the latest primary clutch). (b) The mean values of laying order for primary females and the proportion early monogamous females from a. Outer error bars indicate 1 SD and inner limits (horizontal caps) indicate 95% confidence limits. Figures indicate number of nests. (c) Fledging success of females of different mating status are plotted for the four species with 95% confidence limits. For lapwings, the survival estimate is based on chick survival to day 16 from the 1998 season. Data sources: starlings* (from Smith et al., 1994; data from diagram), starlings** (from Pinxten and Eens, 1990), pied flycatchers (from Stenmark et al., 1988), and blue tits (from Kempenaers, 1994).

significantly higher than that of secondary females (Figure 3c; Stenmark et al., 1988).

### The blue tit

Blue tit data was found in Kempenaers's (1994) study of a nest-box colony near Antwerp, Belgium, during the breeding seasons 1990–1992. From Figure 2e, it is evident that blue tit settlement bears a resemblance to that of pied flycatchers.
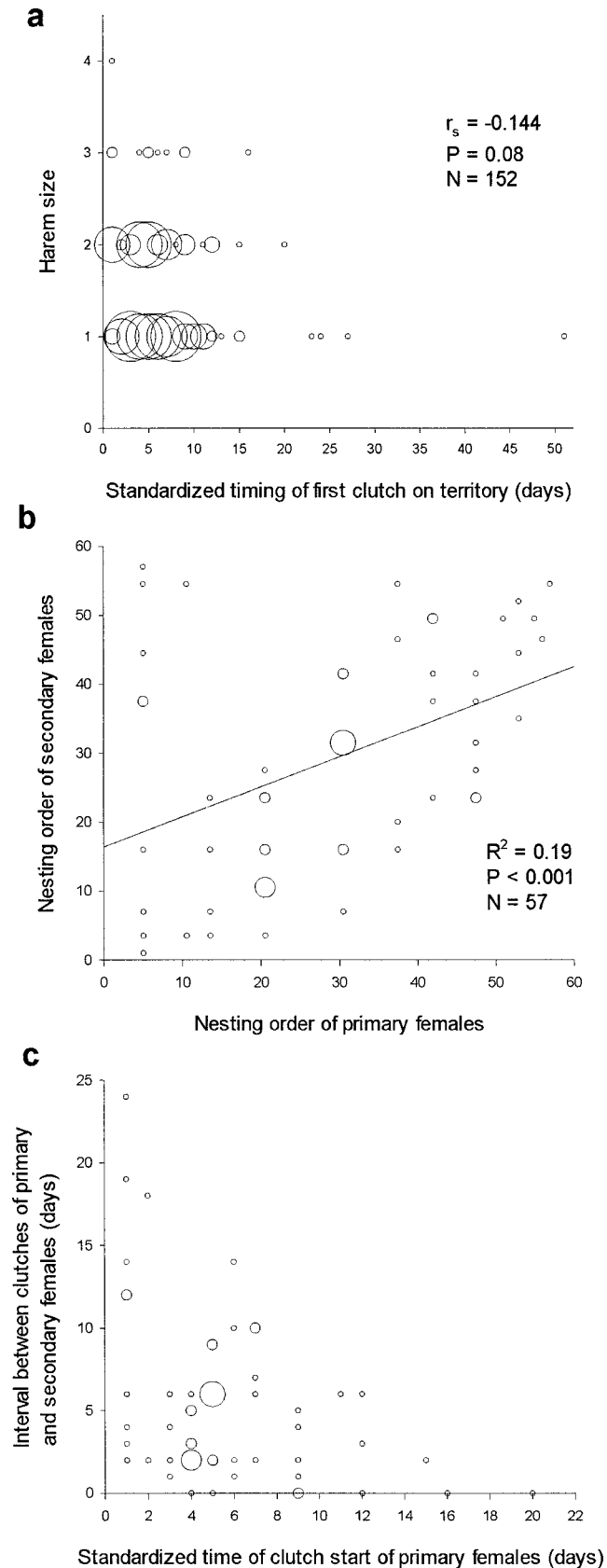
Primary females nested significantly earlier than did monogamous and secondary females, and monogamous females earlier than secondary females, but not significantly so. Seventy-seven percent of the monogamous females nested at the same time as primary females (Figure 3a,b), which was lower than in the other species examined.

There was a significant effect of mating status on fledging success (Kempenaers, 1995). Fledging success was similar in monogamous and primary females, with success in both being higher than that of secondary females (Figure 3c). These observations indicate that also the blue tit settlement pattern might conform to a scenario somewhere between scenarios c and d.

## DISCUSSION

### Main conclusions

Our results show that incorporating varying female quality when modeling settlement produces a range of predictions. Resting on the assumption that early settlers are of higher competitive abilities than later settlers, this model predicts what is commonly found empirically that (1) monogamous females settle earlier than one would expect from the PTM, and (2) secondary females have lower success than monogamous females. Also the variance in settlement date was higher in monogamous than in primary and secondary females in the lapwing. The findings in this study indicate that settlement of lapwings, pied flycatchers, and blue tits conforms to predictions derived from scenario d, and settlement of starlings to scenario d or e. These patterns are expected with the presence of intermediate to large differences in breeding quality among females.

In allowing female arrival order and competitive ability to depend on condition, this model simulates an optimality situation. A late-arriving weaker female has a lower reproductive optimum than that of earlier settlers, and would probably do worse than a primary female or a monogamous female, even if all other extrinsic factors were held equal (i.e., secondary females would probably, despite removal of primary females, do worse than monogamous females, owing to lower optima in reproductive output than those of monogamous females in general). The observed discrepancy with PTM predictions arises because females of different mating status systematically vary in quality and "make the best of a bad job" optimizing in relation to their own intrinsic resources, which may be lower than that of monogamous and primary females.

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**Figure 4**
(a) A Spearman's rank test revealed no significant correlation between day of clutch completion of first nest on the territory (estimate of BSQ) in lapwings. Data from seasons 1991–1996 and 1998–1999. For each season, the day of clutch completion was standardized relative to the earliest nest. Data were then pooled. (b) The rank order of colonization time of primary females correlated significantly with the rank order of colonization time of secondary females. Day of clutch completion was standardized relative to earliest nest in season, and values were then pooled. The rank orders were calculated based on these standardized values. (c) The interval length between primary and secondary females breeding on the same territory plotted against time of clutch start of primary females. The maximum interval lengths and the variance decreased markedly with later breeding start of primary females. A likely explanation for this pattern is that there existed a threshold date, at approximately 20 days after breeding start of the earliest female, after which it was unfavorable to breed.

## Precision of the model

The predictions regarding fitness and settlement order stated in this study are to some extent dependent on the shape of the distribution describing differences in females and in the BSQ of different territories. In this study, we have chosen an exponentially decreasing shape (Figure 1), but alternative distributions describing such a system are also conceivable (e.g., linearly decreasing values, giving roughly similar results). Something resembling our choice of distribution seems plausible to us. However, as empirical data becomes available on this, values derived in Equations 1 and 2 may be substituted with more precise quality estimates.

Another potential source for discrepancy within the model is the extent to which males may work to reduce friction between polygynous females, thus evening out differences in sharing costs between polygynous females. In lapwings, males show this kind of behavior (Grønstøl, 2001), and it is also reported in other studies (for a review, see Slagsvold and Lifjeld, 1994). Individual variation in this characteristic might explain some inconsistencies between the predictions of our model and empirical results.

## Alternative explanations

Other explanations for discordance with PTM predictions that assumes equal competitive abilities of females include sexy-son effects, female-biased sex ratio, and maladaptive choice owing to deception (Alatalo et al., 1981), restricted mate sampling/high search costs (Slagsvold and Lifjeld, 1994; Stenmark et al., 1988), or an unpredictable environment (Wittenberger, 1981).

The sexy-son hypothesis (Alatalo and Lundberg, 1986; Alatalo and Rätti, 1995; Weatherhead and Robertson, 1979, Wittenberger, 1981) states that the lower number of offspring produced by secondary females relative to contemporary monogamous females is offset by the genetic benefits of mating with superior males. Their offspring are thought to inherit the fathers' attractiveness and mating success, resulting in a delayed compensation that, in sum, yields similar fitness to that of the contemporary monogamous breeders. It has been argued that this hypothesis should be rejected on theoretical grounds (Kirkpatrick, 1985), although other investigators argue that it may be valid under certain circumstances (Alatalo and Rätti, 1995). Even if this hypothesis could explain the reduced annual reproductive output in secondary females relatively to monogamous females, it does not explain the relatively early settling dates of monogamous females. If secondary females "went shopping for good genes," one should expect them to settle on the territories of the most attractive males, which should be on the earliest settled territories. One would then expect to see that primary females settled before monogamous females.

Lack of available mating territories and a female-biased sex ratio may constitute reasonable explanations for the lower success of secondary females relative to primary and monogamous females, but this fails to explain why secondary females fail to settle on the earliest chosen territories.

Considering the spatial distribution of nests on polygynous territories, maladaptive choice owing to the mated male deceiving prospecting females (into thinking that he is a bachelor) is not likely to be an important mechanism in lapwings, starlings, and blue tits. In the polyterritorial pied flycatcher, evidence has been presented both in favor and against this kind of mechanism (Alatalo et al., 1981; Slagsvold and Dale, 1994; Stenmark et al., 1988). Maladaptive female choice owing to high search costs and restricted opportunities for mate sampling may occur (Slagsvold et al., 1988; Stenmark

et al., 1988). Radio-tracking data from Sweden revealed that 13 female great reed warblers (*Acrocephalus arundinaceus*) sampled on average six males (with a maximum of 11) before settling (Bensch and Hasselquist, 1992), and a study of pied flycatchers involving video monitoring of prospecting females revealed a median value of 4.5 sampled males (with a maximum of 10). Females sampled up to seven males in 1 h, with minute search costs in terms of time and energy (Dale et al., 1992). Such estimates are likely to be conservative, because it is difficult to accurately follow the complete sampling route of a prospecting female, and to determine when a female has enough information on a male to make a decision for or against settling.

In addition, temporal changes in BSQ between the time of settling and the time of chick fledging could create inconsistencies between theory and empiricism (Wittenberger, 1981). However, the effects of both restricted mate sampling and an unpredictable environment should presumably introduce "white noise" to the system, increasing the variance around the expectation, and not result in a systematic bias pulling in a certain direction.

The assumption underlying the PTM, that females must be of similar quality, is rarely explicitly stated in studies dealing with the PTM and is therefore probably not always considered when testing the model. Krebs and Davies (1993, p. 234) provide an exception, commenting that "The assumptions of the PTM are like those of 'the ideal free distribution' ... [and] ... that ideal free conditions rarely hold in nature because dominant individuals attempt to grab more than their fair share of resources."

## Interaction between female condition and time of breeding

To properly evaluate the impact of the other possible explanations stated previously, one would at least need to successfully control for differences in quality between females of different mating status. Several studies have controlled for seasonal decreasing reproductive output when testing PTM predictions (see Alatalo et al., 1981; Bensch, 1996; Garson et al., 1981; Johnson et al., 1993; Quinn and Holroyd, 1992; Searcy and Yasukawa, 1996; Stenmark et al., 1988). Some studies found that secondary females fare worse than do monogamous females, even after such adjustments, whereas other studies found that after statistically controlling for the seasonal effect, secondary females perform in the range of monogamous females. However, to statistically control for the effect of season by using residuals from a linear regression, or performing an ANCOVA, one must establish that the seasonal reduction in reproductive output is not related to intrinsic differences in quality between early and late breeders. If later-arriving females are of lower quality (see Daan et al., 1988; Drent and Daan, 1980) and if these females end up as secondary females (which generally is true by definition), such a regression would bias the results in a way that artificially overestimates the success of secondary females relatively to monogamous and primary females.

The seasonal decline in reproductive success is probably determined by a combination of both extrinsic and intrinsic factors. To isolate and quantify the effect of intrinsic condition on the seasonal decline, one would have to trap early arriving females, detain them for a period, and then release them to breed. If success of experimentally delayed breeders is similar to that of early breeders and higher than that of contemporary breeders, differences in intrinsic condition should be responsible for the decline in success. If success of delayed breeders is similar to that of contemporary breeders and lower than that of early breeders, the decline should be owing to

extrinsic factors. An intermediate position would indicate an interaction between intrinsic and extrinsic determinants.

## Suggestions for further testing

To further test our framework experimentally, one would need a system/species in which the quantity of finite depreciable BSQ resources could be manipulated in a choice arena for mate-prospecting individuals. Further, there would have to be costs associated with sharing the offered BSQ. One would also need to be able to vary the competitive abilities of prospecting settlers, and to be able to verify or estimate how much of the resources are enjoyed by each of the settlers that share a breeding territory. After having established different scenarios in which the ratio of differences in BSQ among territories to differences in competitive quality of settlers is varied, one might proceed by sequentially introducing settlers to the arena, letting them breed, and subsequently comparing the settlement order and reproductive success with specific, previously generated predictions of the kind presented in this study.

We feel that the approach presented in this study may be fruitful for application in systems in which component costs of polygyny are present. Occurrences of interfemale aggression are regularly or occasionally observed in a range of polygynous systems (Slagsvold and Lifjeld, 1994; and references therein). Such behavior is likely to indicate a cost system that might be suitable for this kind of model. In polygynous species where no important component costs of polygyny are found, other models like the random settlement model may be more appropriate for describing the systems (e.g., bobolink [*Dolichonyx oryzivorus*], Wootton et al., 1986; yellow-headed blackbird [*Xanthocephalus xanthocephalus*], Lightbody and Weatherhead, 1988; corn bunting [*Emberiza calandra*], Hartley and Shepherd, 1995; savannah sparrow [*Passerculus sandwichensis*], Wheelwright et al., 1992; and possibly the red-winged blackbirds, Searcy and Yasukawa, 1995).

If granting that this framework allows for a more precise description of polygynous settlement, there is also a flip side to this approach. Increasing the number of variables in a model increases the number of assumptions that require examination and fulfillment in order to generate predictions that, with necessity, follow from the model. However, we think this cost can be circumvented in several mating systems, and that it is more than counterbalanced by the increased realism gained.

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