

# Experimental confirmation of the polygyny threshold model for red-winged blackbirds

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The polygyny threshold model assumes that polygynous mating is costly to females and proposes that females pay the cost of polygyny only when compensated by obtaining a superior territory or male. We present, to the authors' knowledge, the first experimental field test to demonstrate that females trade mating status against territory quality as proposed by this hypothesis. Previous work has shown that female red-winged blackbirds (*Agelaius phoeniceus*) in Ontario prefer settling with unmated males and that this preference is adaptive because polygynous mating status lowers female reproductive success. Other evidence suggests that nesting over water increases the reproductive success of female red-winged blackbirds. Here we describe an experiment in which females were given choices between two adjacent territories, one owned by an unmated male without any over-water nesting sites and the other by an already-mated male with over-water sites. Females overwhelmingly preferred the already-mated males, demonstrating that superior territory quality can reverse preferences based on mating status and supporting the polygyny threshold model as the explanation for polygyny in this population.

**Keywords:** mating systems; polygyny; polygyny threshold model; *Agelaius*

## 1. INTRODUCTION

A long-standing question in mating systems research is why females in territorial species sometimes choose to settle with already-mated males when doing so lowers their expected share of both male parental help and territorial resources. A variety of answers to this question have been proposed (Searcy & Yasukawa 1989; Ligon 1999), of which the most influential has been the polygyny threshold model (PTM) (Verner 1964; Verner & Willson 1966, Orians 1969). The PTM assumes that there is a cost of polygyny in the sense that a female's expected reproductive success on a given territory is lower if there is another female already present on that territory than if there is not. The model also assumes that female success is influenced by territory or male quality. The model then proposes that females trade the cost of polygyny against the benefit of obtaining a superior territory or mate, settling with an already-mated male only when compensated by obtaining a better territory or mate than they could with any available unmated male.

The PTM was originally formulated in order to explain polygyny in birds, but has since been extended to a variety of other animals (Zabel & Taggart 1989; Dietz & Baker 1993; Schlyter & Zhang 1996), including humans (Borgerhoff Mulder 1990). Despite the great interest evoked by the PTM, critics have pointed out that a strong case for the model has rarely been made (Davies 1989; Ligon 1999). To make such a case, one would need to show that (i) females pay a cost of polygyny and, hence, prefer monogamy, other things being equal, (ii) female choice of mates is influenced by territory and/or male quality, and (iii) the offer of a superior territory or mate will cause females to mate polygynously despite their preference for monogamy. Experimental evidence for each of these points would be preferred to correlative. Point (i) has already been experimentally demonstrated for a population of red-

winged blackbirds (*Agelaius phoeniceus*) in Ontario. Here we test points (ii) and (iii) for the same population.

Secondary females (those choosing already mated males) in many birds obtain less male help with feeding young than do monogamous females (Alatalo *et al.* 1982; Urano 1990; Johnson *et al.* 1993). This alone does not prove a net cost of polygyny because nesting on a territory with other females may also have benefits, for example in reducing nest predation (Ritschel 1985; Picman *et al.* 1988). Secondary females in some polygynous species have lower reproductive success than monogamous and primary females (Alatalo *et al.* 1982; Johnson *et al.* 1993; Slagsvold & Lifjeld 1994). This result is consistent with there being a cost of polygyny, but at the same time weighs against compensation and, hence, against the PTM. In other species, secondary females have reproductive success equal to that of simultaneously breeding monogamous and primary females (Slagsvold & Lifjeld 1994). This result is consistent with there being a cost of polygyny for which females are adequately compensated, but it is also consistent with there being no cost (Searcy & Yasukawa 1989). Thus, in order to test for a cost of polygyny definitively, one needs to manipulate harem sizes experimentally. Only a few such experiments have been carried out under field conditions.

When harem sizes were experimentally reduced in a Pennsylvania population of red-winged blackbirds, the reproductive success of resident females did not change and new-settling females did not prefer smaller harems (Searcy 1988; Searcy & Yasukawa 1995). These results indicate that there is no cost of polygyny in this population. In contrast, when Pribil (2000) manipulated harem sizes in an Ontario population of red-winged blackbirds, females in harems of one had significantly higher reproductive success than females in harems of two. Moreover, in two separate experiments performed in Ontario, female red-winged blackbirds preferred to settle on territories with reduced harem sizes rather than control territories (Hurly & Robertson 1985; Pribil & Picman

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1996). In one of the latter experiments, females were given choices between settling on adjacent territories, one occupied by one female and the other by none. In 16 out of 16 cases, the first female to settle chose the territory on which she would be monogamous (Pribil & Picman 1996). Thus, results on both reproductive success and female preferences indicate there is a cost of polygyny in Ontario populations of red-winged blackbirds, as assumed by the PTM.

Among the many territory attributes that have been examined in red-winged blackbirds, the most consistent correlate of female reproductive success is water depth: nests positioned above deeper water have higher success (Weatherhead & Robertson 1977; Lenington 1980; Picman *et al.* 1993). Females may therefore be expected to prefer territories providing nest sites at greater depths, though to the authors' knowledge this has never been tested experimentally. Here we tested for such a preference using artificial nest platforms that could be positioned at whatever depth was desired. We tested the essential prediction of the PTM, i.e. that females will overcome their preference for monogamy and mate polygynously if compensated by obtaining a sufficiently superior territory, using nest platforms for manipulating territory quality and removals for manipulating harem sizes.

## 2. METHODS

The study was conducted in three marshes near Ottawa, Canada (45°23' N, 75°32' W) in the spring of 1999. The maximum water depths in the three marshes were 90, 105 and 110 cm, respectively. The principal nesting substrate in all three marshes was cattails (*Typha latifolia* and *Typha angustifolia*), which extended from dry land along the shore to depths of up to 1 m. We established a grid of wooden stakes along the shoreline at each marsh and used the grid for drawing detailed maps. We measured water depths at the grid stakes and at intervals between them and used the measurements for plotting isoclines of water depth. Seasonal variation in water depth was monitored in the one marsh where fluctuations occurred. We plotted the territories of male red-winged blackbirds based on observations of their displays and aggressive encounters.

The experiment was designed in order to give female red-winged blackbirds choices between already mated males on superior territories and unmated males on inferior territories. The experiment was begun in late April, when females started settling on the study marshes. We manipulated pairs of adjacent territories (territory dyads). One territory in each dyad was randomly chosen for being improved in quality and the owner of this territory (the mated male) was allowed to retain one mate. The second territory was lowered in quality and all females were removed (the unmated male). The harem sizes on the two sets of territories were similar prior to removals, averaging 1.5 ( $\pm 1.3$  s.d.) females on territories randomly chosen for the mated male set and 1.4 ( $\pm 0.8$ ) females for the unmated male set ( $t = 0.57$  and  $p > 0.50$ ). Territory quality was manipulated using artificial nesting platforms. Nesting platforms were constructed from rectangular wooden frames (40.5 cm  $\times$  44.5 cm). Chicken wire (2.5 cm mesh) was fastened to both the top and bottom of the frame and old cattail shoots (those grown during the previous year) were cut near the ground and their lower ends wedged through both layers of wire. Between 80 and 150 shoots were wedged in one frame,

depending on shoot thickness. Nesting platforms were placed in open water on the territories of mated males and on dry land on the territories of unmated males. Platforms placed in water were anchored to the bottom with wooden stakes so that the top of the frame was below the water surface and the shoots extended above it. The frame was concealed with floating vegetation. Platforms placed on land were lowered into rectangular holes so that the top of the frame was just below the surface of the ground. We placed two to five nesting platforms on each mated male's territory and an equal number on the unmated male's territory. Platforms on both territories were placed in similar spatial configurations. A second part of the manipulation of territory quality was to use a trimmer for cutting any cattails emerging from open water on the territories of both mated and unmated males, except for a small patch (1–3 m in diameter) containing the nest of the resident female on the mated male's territory.

Female removals were initiated in each dyad when the first resident female on the mated male's territory began nest building. We captured all females on the unmated male's territory using a decoy trap (Picman 1979) and also removed their nests. If more than one female was present on the mated male's territory, all but one (randomly pre-selected) were removed, again along with their nests. Removed females were held in cages until the end of the experiment and then released. The removal of females, trimming of cattails and placement of platforms was usually completed in one day. Each dyad was subsequently visited twice a day in the early morning and late afternoon and monitored for the presence of new females and the activities of the resident males and female. We established a total of 19 territory dyads between 6 and 31 May.

## 3. RESULTS

### (a) *Female settlement*

We monitored the dyads from 6 May to 26 June. During this time, 16 dyads were settled by new females and three were not. New females settled on the dyads between 10 May and 3 June, which was one to 20 days (mode = one day) after the dyads were established. After settlement, the females commenced nest building during days 0–8 and egg laying during days 2–11. One of the three dyads attracting no new females was abandoned by the unmated male after eight days and two failed to attract females during 14 and 26 days of monitoring, respectively.

The mated male's and unmated male's territories were settled simultaneously on two of the 16 dyads that were settled, meaning that no females were present on either territory during one visit and that both held a female during the next visit. Female preferences on these dyads cannot be inferred. Only one female arrived on the remaining 14 dyads and was present for at least two consecutive visits before another female appeared. Of these 14 dyads, a female settled first on the mated male's territory in 12 (86%) cases and on the unmated male's in two cases (14%). This settlement pattern is significantly different from random ( $p = 0.013$  by a two-tailed binomial test) in the direction of a preference for already mated males on superior territories over unmated males on inferior territories.

### (b) *Nesting*

All 12 of the females settling on the territories of mated males commenced nest building in the nesting platforms

placed in deep water. Once the females completed a nest base, their nesting activities followed one of three trajectories: (i) eight females completed the nest and laid a clutch, (ii) two females moved to the upland portion of their mate's territory, built a nest and laid a clutch, and (iii) two females disappeared four and five days after settlement, respectively. A female appeared five days later on one of these last two territories and built a nest in the upland portion of the territory, but, because females were not banded, it is not certain whether this was the original female returning or a new female. All eight females that nested on platforms on mated male's territories successfully fledged young.

One of the two females settling on the territories of unmated males initiated nest building in a land platform but then abandoned that nest. The other built a nest in the upland portion of her mate's territory and laid a clutch. Her nest was depredated shortly afterwards.

#### (c) *Compensation*

The PTM predicts that females will only choose already mated males if the territories of those males are sufficiently superior to make that choice adaptive. Female red-winged blackbirds in this population lay an average of 3.41 eggs ( $n=204$  females). Losses due to inclement weather, hatching failure and starvation average 1.08 eggs or young, so in the absence of predation females can expect to fledge 2.33 young. The probability of nest predation declines sharply with increasing water depth from 0 to 30 cm and then levels off asymptotically (S. Pribil, unpublished data). In our study, platforms on mated male territories were placed at a mean depth of 58 cm, where predation averages 21% (six out of 29 nests) and platforms on unmated male territories were placed in 0 cm of water, where predation averages 65% (42 out of 65 nests). Females can therefore expect to fledge  $(1-0.21) \times 2.33 = 1.84$  young nesting on water platforms and  $(1-0.65) \times 2.33 = 0.82$  young nesting on shore platforms. The difference (1.02 young) estimates the benefit of nesting over water.

This benefit must be compared to the cost of polygyny. In a study in which harem sizes were experimentally manipulated (Pribil 2000), 40 secondary females on bigamous territories fledged a mean of 0.221 young per egg compared to 0.403 young per egg for 40 females on monogamous territories. Therefore, if both monogamous and secondary females laid the population mean clutch size of 3.41 eggs, monogamous females would produce  $0.403 \times 3.41$  or 1.37 young compared to  $0.221 \times 3.41$  or 0.75 young for bigamous females. The estimated cost of polygyny is therefore  $(1.37-0.75)$  or 0.62 young. Thus, the benefit of nesting over water (1.02 young) is greater than the cost of polygyny (0.62 young). We modelled the balance between cost and benefit using a simulation in which both the probabilities of nest failure over water and over land and the numbers of young produced per egg for monogamous and secondary females were chosen randomly from the observed distributions. The reproductive success of secondary females nesting over water was equal to or greater than the reproductive success of monogamous females nesting over land in 88% of 10 000 runs of the model.

## 4. DISCUSSION

In our study, territory quality influenced the mating preferences of female red-winged blackbirds. Females preferred to settle on the territories of mated males with over-water nesting platforms rather than on the territories of unmated males with over-land nesting platforms in 12 out of 14 dyads where a choice was made. This settlement pattern was significantly different from random, but a random pattern may not be the most appropriate comparison. Pribil & Picman (1996) found that female red-winged blackbirds in the same area unanimously preferred unmated males to mated ones (16 out of 16 cases) when neither territory was manipulated. Hence, in our experiment, manipulating territory quality reversed the usual strong preference for unmated males to yield an almost equally strong preference for mated males. The difference in outcomes between the two experiments (12 out of 14 females choosing already mated males versus none out of 16) is highly significant ( $\chi^2=22.9$  and  $p < 0.0001$ ). Further, our evidence suggests that the preference for mated males with superior territories is adaptive in that females on average should have higher reproductive success nesting as secondary females on territories with over-water nest sites than as monogamous females on territories without over-water sites. In sum, we have experimentally shown that females reverse their preference for unmated males if adequately compensated by obtaining a superior territory with an already mated male. This is the essence of the PTM.

Davies (1989), Ligon (1999) and others have criticized the PTM on the grounds that few studies have provided strong support for the hypothesis. A recent exception is the study of Slagsvold & Drevon (1999), which showed that female pied flycatchers (*Ficedula hypoleuca*) choosing in aviaries preferred unmated males but would choose mated males if the mated males themselves were of higher quality. There is convincing, non-experimental evidence in a few species that females pay a cost of polygyny and that they choose already mated males when those males offer superior territories, for example in great reed warblers (*Acrocephalus arundinaceus*) (Bensch 1996; Hansson *et al.* 2000) and certain human populations (Borgerhoff Mulder 1990). Nevertheless, it is clear that the PTM is not the universal explanation for polygyny that it was once hoped to be, not even for birds. Alternative explanations that may apply equally often are random settlement due to the absence of a cost of polygyny (Lightbody & Weatherhead 1988; Hartley & Shepherd 1995; Friedl & Klump 2000) restricted mate sampling (Stenmark *et al.* 1988; Slagsvold & Dale 1994) and maladaptive choice (Johnson *et al.* 1994).

Two of the females in our sample chose an unmated male without overwater nest sites even though this choice seemed on average to be maladaptive. One explanation for their behaviour is that they happened to encounter an unmated male with an unusually good territory in other respects, so that the specific choices they made were actually adaptive. Our simulation suggests the unmated male is the superior choice in a minority of instances under the conditions of the experiment, but whether females can predict these cases is unknown. Another explanation is that the choices of these two females were influenced by

aggression from the resident females on the territories of the mated males in the dyads they encountered. Female–female aggression in these circumstances is well known in red-winged blackbirds (LaPrade & Graves 1982; Yasukawa & Searcy 1982). We observed such aggression in five of our dyads, including one of those in which the first-settling female chose the unmated male. Experimental evidence suggests that female–female aggression affects settlement in some polygynous birds (Sandell & Smith 1996; Slagsvold *et al.* 1999) and it has been suggested that this behaviour has a major impact on the occurrence of polygyny (Slagsvold & Lifjeld 1994). This impact is of course negative, as female aggression limits rather than promotes polygyny.

The PTM was proposed over 30 years ago (Verner 1964; Verner & Willson 1966; Orians 1969) and remains one of the most elegant hypotheses in behavioural ecology. The assumptions of the hypothesis are more restrictive (Davies 1989) than was at first realized so that its application is not as wide as was once hoped. Nevertheless, our work and that of others has demonstrated that the PTM can be a powerful and satisfying explanation for the occurrence of polygyny.

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