

How Polygynous Female Northern Harriers *Circus cyaneus* Choose their Mates and Why they are Deceived

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Female choice has become a focus of attention (Bateson 1983) because it can give an insight into why particular mating systems occur among particular species. For example, because Northern Harriers (*Circus cyaneus*) practise resource defence territoriality, it is likely that females choose males on the characteristics of the defended territory, and this in turn can give some idea as to why some females choose polygyny over monogamy.

In order to determine which cues are important for female harriers, one can use the following three-part process: (1) identify factors that limit female fecundity - either through their effect on the success or failure of the nest, or if successful, the number of young surviving to fledging; (2) ask if such limiting factors can be assessed by pre-settling females, are reliable indicators of future success (or at least covary with these indicators) and vary between breeding situations. If so, then it is possible that such cues could be used by females in their mate choices. Finally, (3) if one assumes that females will generally choose the best remaining sites first, one can then correlate each of the possible cues with the order in which females settled to determine which cues females actually used (Lenington 1980). I used this approach to determine why polygynous female harriers in Canada chose polygyny over monogamy, what cues they used, and why they ultimately fared so poorly (Simmons *et al.* 1986a).

I have previously ruled out the "sexy-son" hypothesis (Weatherhead & Robertson 1979) because those females choosing mated males (hereafter polygynous females or β , γ and δ females) suffer losses too high for their sons to recoup in the first one or two generations, and also the possibility (Elliot 1975) that females enjoy increased longevity in harems, because there are no obvious benefits to harem living that increase either the females' survival or that of their progeny. Furthermore, the popular idea (e.g. Balfour & Cadbury 1979; Newton 1979; Picozzi 1984) that skewed sex ratios constrain potential breeders among females to mate with already mated males because there are no other options (except non-breeding) can be ruled out for Northern Harriers because polygyny arises not just at the end of the season (when one would expect all available bachelors to have mated - and hence some constraint) but evenly throughout (Simmons 1983). More importantly, some males acquire more than one mate (up to five) before others have attracted one, so differences in male quality or controlled resources are implied (Simmons *et al.* 1986a). Thus Northern Harriers appear to conform to the competitive female choice model of Verner (1964) and Orians (1969); this model assumes that females compete for resources, choose breeding sites on the basis of territory or male phenotypic characters, and are normally unconstrained in their choices by a shortage of males.

Female harriers choose mates on the basis of the following characters: (a) nest sites - harrier ground nests are highly vulnerable to terrestrial predators and vary in quality (Simmons & Smith

1985); (b) feeding territory quality - females forage within male-defended territories of variable quality for up to 4 weeks (Simmons *et al.* 1986a); and (c) paternal investment in provisioning and defence - males not only defend nests vigorously, but provide the bulk of food to their incubating mates and young (Hamerstrom 1969, Simmons *et al.* 1986b).

Does nest site quality make any difference to success or failure of harrier nests? Yes, based on moisture at the nest, female harriers could increase their chances of success by up to 90% by choosing the wettest nest sites. Did females in fact use this potentially highly reliable cue? No, in 1980, 1981 or 1982 there was no correlation between the order in which females settled and nest site quality. Hence females did not appear to choose mates on the basis of nest site quality.

Male nest defence made little difference to nest success (Simmons *et al.* 1987), and is thus considered an unimportant cue for females.

The second component of fecundity, the number of young surviving to day 30 (brood survival) is potentially affected by the quality of the females' feeding territory (if the female is left to feed the young) and the males' provisioning performance. Did either aspect significantly affect brood survival? While the quality of the female feeding territory bore no relationship with brood survival ($r=0.1$ and 0.03), male provisioning, expressed as food items delivered/14-h day, was consistently the strongest predictor of young reared ($r=0.82$ in both years).

Did females then choose mates on the basis of this cue - assessable through supplementary (courtship) feeding? Unlike nest site quality, strong correlations existed between settling order and male provisioning rates ($r_{1980}=-0.65$, $p=0.02$; $r_{1981}=-0.84$, $p=0.002$). That this occurred in both years strongly suggests that females were basing their choice of mate on food provisioning, and not on nest site quality; females were apparently maximising brood survival, not minimising complete failure.

Despite this, polygynous females reared significantly fewer young ($x=0.88 \pm 1.7$) than monogamous females settling at the same time ($x = 3.25 \pm 1.4$, $t=3.58$, $p < 0.01$). The ratio (x) of polygynous to monogamous female productivity (0.27) is the lowest published value for any avian polygynist.

These results are paradoxical: despite choosing mates and their provisioning rates so as to maximise brood survival, all but polygynous females then realised this expectation. In other words, using the same cue (male provisioning rate), both alpha and monogamous females reproduced significantly better than polygynous females. This suggests that provisioning rates were unreliable indicators for polygynous females. In reality, male harriers are known to concentrate their seasonal food supply to first-settling females (Simmons *et al.* 1986a), but polygynous females cannot be expected to predict that a male's provisioning rate may later decline if this cue is normally used (successfully) by all other females. Females do not appear to learn through experience, since most females in harems were old birds (*ibid*).

If polygynous male harriers acquire further females through deceptive provisioning (i.e. providing false information about their future paternal assistance), their initial provisioning (courtship) rate should be similar to that offered to monogamous or first-settling females. Because *seasonal* (incubation + post-hatching) and not courtship rates were monitored, I calculated the provisioning rate that a polygynous female "expected" from her clutch size. Clutch size and courtship provisioning are causally related in at least two temperate zone raptors (Newton & Marquiss 1981; Dijkstra *et al.* 1982) and, indeed, clutch sizes of monogamous females were significantly related ($r=0.79$, $p < 0.01$) to "expected" (seasonal) provisioning rates of male harriers in New Brunswick. Thus I predicted expected provisioning rates for polygynous females using the following equation: $FOOD = 3.30 + 1.42 (EGGS) - 0.043 (DAY)$. As predicted, observed provisioning rates for polygynous females (Table 1) were significantly lower than those they expected ($t=4.14$, $p < 0.005$); this supports the idea that males fed polygynous females as much food as other dependent females, yet later deserted them in favour of alpha females. Since I have shown that feeding rate is the principal mate choice cue used by female harriers, I suggest that males have exploited this dependence and feed extra females whenever they can, in order to obtain extra mates. I label this deceitful because males are not capable of sustaining such rates. Females choosing a bachelor male with a similar courtship rate, however, would have received the paternal assistance such rates would have promised.

The polygyny-by-deceit scenario further predicts that, as food abundance increases, more males should exceed the courtship provisioning polygyny threshold, and thus variations in the frequency of polygyny should parallel variations in harrier food abundance (see also Newton

1979). This was verified; strong, significant correlations existed between vole abundance and male polygyny over 5 years in New Brunswick (Simmons *et al.* 1986b). Food abundance and male provisioning in particular thus appear to be the principal factors influencing polygyny in Northern Harriers.

Table 1. Provisioning rates expected by polygynous females (predicted from knowledge of their clutch size and laying date) relative to that observed. Observed and expected rates differed significantly.

Female	Harem position	Clutch size	Initiation date	Provisioning rate expected	Provisioning rate observed
1	β	5	7 May	10.1	7.6
2	γ	5	18 May	9.6	2.5
3	β	5	20 May	9.5	4.8
4	γ	4	9 June	7.3	1.5
5	β	4	8 June	7.3	4.2

I conclude that female harriers base their choice of mate principally on male provisioning performance, and some females choose mated males because certain males deceitfully provision them large amounts of courtship food and later desert them in favour of alpha females. Consequently, unassisted females rear significantly fewer young than monogamous and alpha females. Thus polygyny is maladaptive to secondary females, but is maintained primarily through male deceit.

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