

HONEST ADVERTISING, SEXUAL SELECTION, COURTSHIP DISPLAYS, AND BODY CONDITION OF POLYGYNOUS MALE HARRIERS

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ABSTRACT.—In polygynous Northern Harriers (*Circus cyaneus*) aerial displays reflect male body condition, and displays are therefore difficult to fake. The most vigorously displaying males attract the largest harems, and such displays are an accurate measure of a male's potential to provision their mates (the single most important influence on female fecundity). Whether females preferentially pick intensely displaying males because they are in better condition or because vigorous displays are associated with higher provisioning rates is unknown, but evidence suggests that both condition and provisioning are important mate-choice cues. I conclude that sexually selected behavior in harriers is largely consistent with the honest-advertising hypothesis. Received 17 August 1987, accepted 21 December 1987.

FISHER'S (1930) model of "runaway" sexual selection has been challenged because models based on female choice do not take account of problems associated with the low heritability of characters chosen by females (e.g. Gustafsson 1986). This led Kodric-Brown and Brown (1984) to suggest that selection has favored the evolution of costly phenotypic traits, which reflect genotypic quality. Thus, rather than abstract epigamic traits alone influencing female choice (e.g. Darwin 1871, Andersson 1982), females may use cues such as tail length as "truthful" markers of genetic quality. Similarly, Andersson (1986) suggested that if secondary sexual traits mirror an organism's nutritional status, and nutritional status reflects genotypic quality, then no initial mating advantage is necessary for Fisherian sexual selection to evolve. There is essentially no difference between these hypotheses other than the emphasis that Kodric-Brown and Brown (1984) put on exaggerated physical traits such as antlers and nuptial coloration and Andersson's (1986) emphasis on body condition and nutritional status as a reflection of genotypic quality.

In lek species that defend no resources, viability differences may be advertised through body condition, vigorous displays, or even tail length (Andersson 1986). For resource-defending species, sexually selected behavior may be an advertisement of resource quality (Searcy 1979) and possibly body condition. Thus, females may prefer intensely singing or displaying males because of the direct resource benefits

that will enhance their lifetime fitness (Searcy and Andersson 1986).

Assessing the Kodric-Brown and Brown/Andersson model for resource-defending species is possible by establishing correlations between display vigor and body condition, assessing the relative quality of controlled resources or male investment and correlating them with display vigor, and determining whether close associations exist between display vigor and harem size (polygynous species) or temporal differences in mate attraction (monogamous species). Although sexual displays such as song intensity or song rate are closely correlated with paternal feeding, superior territories, and paternal nest defense in Red-winged Blackbirds (*Agelaius phoeniceus*) and Stonechats (*Torquata saxicola*) (Greig-Smith 1982, Searcy and Yasukawa 1983), no such data exist for birds that lack acoustical displays. I present evidence that the most actively displaying male Northern Harriers (*Circus cyaneus*) attract the largest harems, that such intersexual displays cannot be faked because they appear body-condition dependent, and that they accurately advertise at least a male's potential to provision his mates.

STUDY AREA AND METHODS

I studied a large population of breeding Northern Harriers in New Brunswick, Canada, from 1980 to 1982. All nests were monitored, and variables such as the quality of female foraging areas, nest sites, and male provisioning and male nest defense were recorded concurrently (details are given by Simmons

and Smith 1985, Simmons et al. 1986b). In addition, all aerial courtship displays by adult and young (<3 yr) males were recorded throughout three breeding seasons, based on approximately 900, 700, and 900 h observation. I am confident that almost all displays were recorded because the spectacular nature and flashing gray-white effect of the males involved made the displays highly visible. Furthermore, several males were monitored simultaneously during 562 h of observation at specified nests. Each display comprised a sequence of deep U-shaped undulations covering a distance of up to 1 km at a height of 10–300 m (see Watson 1977: 114 for descriptions). In New Brunswick the sequences comprised 2–74 continuous Us and were directed, in all but a few instances, at flying or perched females. Most displays were recorded in early May, the egg-laying/incubation phase of harrier breeding (see Simmons et al. 1987). I scored displays on the basis of both total number of Us and the number of sequences per male. Males were not marked because trapping caused temporary nest desertion. I assumed each male controlled the territory over which he displayed and in which he invariably landed. Intruding males invading known territories were quickly escorted out, and neighbors rarely infringed territorial boundaries.

Food-abundance indices.—Populations of Meadow Voles (*Microtus pennsylvanicus*) were monitored on the marsh as an index of annual food abundance. As the harriers' principal prey (Barnard et al. 1987), voles influence almost every aspect of harrier reproduction, from breeding numbers (Hamerstrom 1979) and clutch size to behavior (Simmons et al. 1986a) and polygyny (Hamerstrom et al. 1985, Simmons et al. 1986a). I examined Andersson's (1986) condition-dependent female preference hypothesis under the premise that males should be in better condition in vole-high years and therefore should display more vigorously.

Resource quality and male investment.—To determine if males were "truthfully" advertising the quality of resources such as paternal assistance, nest sites, and foraging areas, I compared each resource with reproductive success for an index of quality and then correlated quality with harem size. Safe nesting areas and high provisioning rates are important to nesting harriers (Simmons and Smith 1985, Simmons et al. 1986b), but neither the extent of male nest defense nor the quality of female foraging areas (Simmons in press) significantly influence reproduction. Thus, resource quality is based on nest sites and male provisioning alone. Provisioning of females by males, which begins before egg laying and continues throughout the nestling period (Simmons et al. 1987) was documented for 9 males each year, based on 562 h of nest observations. Rates are expressed as items per day, not biomass, because no discernible differences in prey sizes were evident within years.

Nest-site quality scores (Simmons and Smith 1985) were based on the probability of nest success in three

substrates: Dry, Wet, and Very Wet areas. Harrier ground nests were less susceptible to terrestrial predators in the wettest areas. Annual reproductive success, the number of young reared to first flight, was used as an index of lifetime success because the two are closely correlated in at least one other raptor (Newton 1985).

RESULTS

Food abundance and display frequency.—Vole population indices decreased by a factor of 13 during the study, from a high in May 1980 to a low in May 1982. The frequency of two important male behaviors paralleled this decline. Nest defense decreased by a factor of 3 (Simmons et al. 1986a), and male courtship displays decreased from 43 display sequences (comprising 573 Us) to 6 sequences (comprising 37 Us). Average display frequencies per male, a better measure of the decline in displays, decreased from 2 sequences (27.3 Us) per breeding male in 1980 to 0.5 (3.1 Us) in 1982. Moreover, yearling males did not display at all in the food-poor years but were present and temporarily territorial in all years (Simmons et al. 1987).

Display frequency and harem size.—Males that displayed most often and vigorously attracted, and bred with, significantly more females than weakly displaying males (Fig. 1). Both the number of sequences ($r = 0.741$, $P < 0.01$, $n = 14$) and the number of individual Us executed by each displaying male ($r = 0.551$, $P < 0.05$, $n = 14$) were correlated with harem size. This is a conservative measure of the influence of displays on mate attraction because monogamous males that never displayed were not included.

A direct test of the idea that display rate is an accurate advertisement of provisioning rate is impossible because of the small number of males for which both displays and provisioning were recorded ($n = 6$). I assumed that most males with large harems displayed vigorously and investigated the correlation between harem size and resource quality.

Harem size, nest-site quality, and provisioning performance.—The eggs and nestlings of harriers are vulnerable to terrestrial predators, and nest-site quality plays a significant role in nest success (Simmons and Smith 1985). Although nest-site quality scores were generally higher for polygynous males (Table 1), the trend was not consistent. Bigamous males controlled the highest-quality areas, and the quality scores did not differ significantly among males (Table 1).

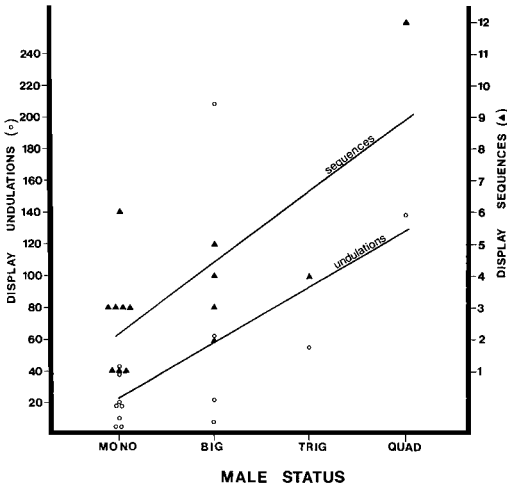


Fig. 1. Mated status of male Northern Harriers in relation to courtship displays. Courtship displays are graphed as the number of sequences (bouts), and as the total number of U-shaped undulations. Both measures were related significantly to harem size.

Thus, males did not appear to be advertising high-quality nest sites, and females were unlikely to be using display vigor as a cue for nest-site quality.

Polygynous males, however, had significantly higher provisioning rates per day (12.98 ± 4.7 , $n = 4$) than monogamous males (8.58 ± 3.1 , $n = 16$; $t = 2.3$, 18 df, $P < 0.05$), matching previous findings for male European Marsh Harriers (*C. aeruginosus*; Altenburg et al. 1982). This supports the idea that males that attracted the largest harems were also able to sustain higher overall provisioning rates. The possibility that polygynous males provisioned at higher rates simply because there were more females to feed is unlikely because no decrease in rate was observed when secondary females failed (unpubl. data), or when males abandoned these birds in favor of alpha females (Simmons et al. 1986b).

Harem size and male reproductive success.—A prerequisite for sexual selection on males, and in particular male behavior, is that variance in male success should be relatively high (Payne 1979). I found that males reared 0–10 young, while females reared 0–5 young (Simmons et al. 1986b). More importantly, males that attracted more than one female reared significantly more young (4.00 ± 3.0 , $n = 7$) than monogamous males (2.47 ± 1.6 , $n = 38$; $t = 2.00$, 43 df, $P < 0.05$). Intense sexual selection is thus expected to act on male harriers.

TABLE 1. Average nest-site quality scores for males with different-size harems, 1980–1982. No significant differences were found (ANOVA $F_{3,60} = 0.60$, not significant).

Number of mates	Number of cases	QS ^a ± 1 SD
1	45	60.9 ± 11
2	11	65.2 ± 9
3	3	62.8 ± 13
4	5	64.9 ± 9.7

^a QS = quality score; see Simmons and Smith (1985) for sample calculations.

DISCUSSION

I found that males in food-rich years displayed more vigorously than in food-poor years, and males that displayed most vigorously attracted the largest harems. Males that attracted more than one mate also had higher provisioning rates than monogamous males, and hence may have advertised this potential through their displays.

Honest advertising.—To verify that males were “honestly” advertising their condition, one must show that only males in good condition displayed vigorously. Three lines of evidence support this idea. First, male courtship displays decreased as food abundance decreased. Second, second-year males, which are expected to be in poorer condition because they forage less successfully than adults (Bildstein 1978: 215), did not display at all in poor vole years. Finally, the vigor with which males defended their nests also decreased in parallel with food abundance (Simmons et al. 1986a). Each of these male factors, in conjunction with the fact that females produced significantly smaller clutches in food-poor years (Simmons et al. 1986a), supports a condition-dependent basis for the declines in behavioral displays. Possible alternatives, such as that males displayed more often because more females were present in vole-high years (“female-stimulation effect”) or that males simply had more time in which to display in food-rich years, are unlikely for two reasons. First, censuses in Wisconsin indicate that similar numbers of harriers pass through in all years but that more females stay to breed in vole-rich years (Hamerstrom 1969). Hence, if similar numbers of females occur at the season’s start, the female-stimulation effect predicts similar number of male displays between years. This was not so; displays increased as voles in-

creased. Furthermore, the female-stimulation effect cannot account for the increase in male defense scores in food-rich years (Simmons et al. 1986a). Second, if breeding males had more time to display in food-rich years, one would expect no annual difference in display rates for nonbreeding males with no provisioning duties. This was not so. Nonbreeding, second-year males displayed in only 1 of the 3 years. This idea presupposes that displays are not energetically expensive, an unlikely assumption in light of the length and vigor of some displays. In sum, vigorously displaying males appear to be in the best physical condition, and females could use displays as a faithful guide to male condition. That they did so is suggested by the correlations between harem size and display vigor.

My results support the contention that males are advertising their provisioning potential and not high-quality nest sites, but it remains unclear whether females choose males on the basis of body condition or provisioning potential. The simplest explanation is that females use both cues. Displays may act as a first index to a phenotypically high-quality male, while provisioning performance could be used as a more immediate cue to the future performance of each male. These possibilities are supported by findings that females desert poorly provisioning males (Simmons et al. 1987) and that significant correlations exist between male provisioning rate and female settling order (Simmons in press).

If male body condition is reflected in display rate and female harriers use male display as an accurate guide to provisioning potential, then a consequence of the truth-in-advertising hypothesis is that older males would tend to attract the largest harems; they are more successful foragers (Bildstein 1978, Toland 1986) and should have higher provisioning rates than youngsters. This was verified for male harriers in Orkney, which attract larger harems as they age (Picozzi 1984). Therefore, harriers satisfy at least two components of the honest-advertising hypothesis: displays appear to reflect body condition truthfully and may in turn be a first indication of a male's provisioning potential. Despite these conclusions, the subsequent performance of later-settling harem females indicates that male harriers appear to deceive them about future provisioning ability (Simmons in press). Males may switch their full attention back to the alpha female, which increases the

likelihood of both nestling starvation and nest predation for polygynous females (Simmons et al. 1986b). At first glance, these results appear incompatible as males truthfully advertise their condition and resources, yet later desert some of their mates. This is explicable if we remember that for all species with a temporal lag between choice and realized reproduction, choices are based on potential resource quality and not known resource quality (cf. Wittenberger 1981). Even if poor- and good-condition birds display vigorously, only good provisioners can fake high courtship rates to several females. Honesty is therefore conditional.

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LITERATURE CITED

- ALTENBURG, W., S. DAAN, J. STARKENBERG, & M. ZILJSTRA. 1982. Polygamy in the Marsh Harrier, *Circus aeruginosus*: individual variations in hunting performance and number of mates. *Behaviour* 79: 272-312.
- ANDERSSON, M. 1982. Female choice selects for extreme tail length in a widowbird. *Nature* 299: 818-820.
- . 1986. Evolution of condition-dependent sex ornaments and mating preferences: sexual selection based on viability differences. *Evolution* 40: 804-816.
- BARNARD, P., B. MACWHIRTER, R. SIMMONS, G. L. HANSEN, & P. C. SMITH. 1987. Timing of breeding and the seasonal importance of passerine prey to breeding Northern Harriers (*Circus cyaneus*). *Can. J. Zool.* 65: 1942-1950.
- BILDSTEIN, K. L. 1978. Behavioral ecology of Red-tailed Hawks (*Buteo jamaicensis*), rough-legged Hawks (*B. lagopus*), Northern Harriers (*Circus cyaneus*), American Kestrels (*Falco sparverius*) and other raptorial birds wintering in south central Ohio. Ph.D. dissertation, Columbus, Ohio State Univ.
- DARWIN, C. 1871. *The descent of man and selection in relation to sex*. London, Murray.
- FISHER, R. A. 1930. *The genetical theory of natural selection*, 2nd ed. New York, Dover Publ.

- GREIG-SMITH, P. W. 1982. Song rates and parental care by individual male Stonechats (*Saxicola torquata*). *Anim. Behav.* 30: 245-252.
- GUSTAFSSON, L. 1986. Lifetime reproductive success and heritability: empirical support for Fisher's fundamental theorem. *Am. Nat.* 128: 761-764.
- HAMERSTROM, F. 1969. A harrier population study. Pp. 367-383 in *Peregrine Falcon populations: their biology and decline* (J. J. Hickey, Ed.). Milwaukee, Univ. Wisconsin Press.
- . 1979. Effect of prey on predators: voles and harriers. *Auk* 96: 370-374.
- , F. N. HAMERSTROM, & C. J. BURKE. 1985. Effect of voles on mating systems in a central Wisconsin population of harriers. *Wilson Bull.* 97: 332-346.
- KODRIC-BROWN, A., & J. H. BROWN. 1984. Truth in advertising: the kinds of traits favored by sexual selection. *Am. Nat.* 124: 309-323.
- NEWTON, I. 1985. Lifetime reproductive output of female Sparrowhawks. *J. Anim. Ecol.* 54: 241-253.
- PAYNE, R. B. 1979. Sexual selection and intersexual differences in variance in breeding success. *Am. Nat.* 114: 447-452.
- PICOZZI, N. 1984. Breeding biology of polygynous Hen Harriers *Circus c. cyaneus* in Orkney. *Ornis Scandinavica* 15: 1-10.
- SEARCY, W. A. 1979. Female choice of mates: a general model for birds and its application to Red-winged Blackbirds. *Am. Nat.* 114: 77-100.
- , & M. ANDERSSON. 1986. Sexual selection and the evolution of song. *Annu. Rev. Ecol. Syst.* 17: 507-533.
- , & K. YASUKAWA. 1983. Sexual selection and Red-winged Blackbirds. *Am. Sci.* 71: 166-174.
- SIMMONS, R. E. In Press. How polygynous female Northern Harriers choose their mates and why they are deceived. Abstract in Proc. 3rd World Conference on Birds of Prey. Cambridge, England, Int. Council for Bird Preservation.
- , P. E. BARNARD, & P. C. SMITH. 1987. Reproductive behaviour of *Circus cyaneus* in North America and Europe: a comparison. *Ornis Scandinavica* 18: 33-41.
- , B. MACWHIRTER, P. E. BARNARD, & G. L. HANSEN. 1986a. The influence of microtines on polygyny, productivity, age and provisioning of breeding Northern Harriers: a 5-year study. *Can. J. Zool.* 64: 2447-2456.
- , & P. C. SMITH. 1985. Do Northern Harriers (*Circus cyaneus*) choose nest sites adaptively? *Can. J. Zool.* 63: 494-498.
- , ———, & R. B. MACWHIRTER. 1986b. Hierarchies among Northern Harrier (*Circus cyaneus*) harems and the costs of polygyny. *J. Anim. Ecol.* 55: 755-772.
- TOLAND, B. 1986. Hunting success of some Missouri raptors. *Wilson Bull.* 98: 116-125.
- WATSON, D. 1977. *The Hen Harrier*. Berkhamsted, Poyser.
- WITTENBERGER, J. F. 1981. Time: a hidden dimension in the polygyny threshold model. *Am. Nat.* 118: 803-822.

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