

and females, and the males are more competitive than females. In fact, the males are more competitive than females in all species examined except one, and the females are more competitive than males in only one species examined. The results are summarized in the following table, which shows the mean competition scores for males and females in each species.

Table 6.1 shows the male and female competition scores for each species, according to the source of the competitive stimulus. The first two columns give a complete list of the species examined, and the third column gives the mean competition score for each sex. The data are also presented in a bar chart, where the mean competition scores for males and females are shown separately. The chart clearly illustrates that males are more competitive than females, and that females are more competitive than males in only one species.

It is interesting to note that the competition scores for males and females are relatively stable, although there is some variation between species.

DISCUSSION

As we have seen, males are more competitive than females in all species examined. This finding is consistent with the general expectation that males are more competitive than females. However, it is important to note that the competition scores for males and females are not always the same. In fact, in some species, the competition scores for males and females are very similar. This suggests that the competition scores for males and females are not necessarily the same.

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6 *Sexual selection: Mate choice*

Darwin distinguished between two processes in his original formulation of sexual selection [137]. The first we have just considered at length: competition for mates among the members of one sex, usually males. The second sexual selective process is the exercise of mate choice, usually by females.

CHOOSEY FEMALE, INDISCRIMINATE MALE

Throughout the animal kingdom males generally woo females, rather than the reverse. We saw in Chapter 5 why males are usually the more competi-

tive sex and why they are concerned to maximize matings, while females are not. Michael Ghiselin has aptly labeled this element of the male strategy "the copulatory imperative" [212]. As much concerned with quantity as with quality, males are often rather indiscriminate in courtship, but the female's situation is different.

There is a basic strategic difference between the sexes that demands that the female be more discriminating in her sexual responsiveness. Consider the consequences for each partner of participating in a bad mating, one that is unlikely to produce viable, fertile offspring. It is a bad mating, for example, if the mate is of the wrong species or suffers from a genetically based defect that is likely to hinder survival or reproduction. If a male indulges in such a mating, he wastes some sperm. Sperm are relatively cheap. The loss will not diminish his future reproductive possibilities should a better mate appear tomorrow or next week or month. A possibility, albeit slight, that he will sire fertile offspring and perpetuate his genes is worth the investment of a few sperm, and natural selection should have inclined him to make that investment.

The female is in a different situation. The penalty she incurs from a bad mating is likely to be severe. Her great parental investment in each of her potential progeny necessitates that she choose her mate well. Having mated badly, her future reproductive possibilities are diminished. She may not be in a position to accept a better mate should one present himself subsequently: Months of nurture may be committed to an inviable or infertile hybrid. As we might then expect, females are generally more selective than males in their choice of mates. Bateman was aware that the females are mainly responsible for maintaining reproductive isolation between related species of fruit flies. Males will court females of other species as readily as their own. It is the females' task to check the males' credentials. Among invertebrates as diverse as butterflies and hermit crabs males are apt to court an astonishing variety of objects, indeed almost anything that bears some resemblance to a female.

In the vertebrates, with their more complex capabilities for perceiving and processing information, males are seldom quite so indiscriminately eager. Nevertheless, the task of fine discrimination and the prevention of bad matings continues to reside mainly with the females, just as we would expect from considering the differential penalties that such bad matings impose upon the two sexes. Naïve male guppies, for example, are willing to court females of the wrong species, but even naïve females will not accept the wrong males [382]. The males learn to confine their attentions to the appropriate females only by being rejected when they err. Females cannot afford to learn by trial and error, for the errors would be too costly. We could cite further examples of the greater discriminatoriness of the female sex of

various birds and mammals too, but it will perhaps suffice to note that the principle also holds up in our own species. Men are much more susceptible than women to misdirected sexual behavior, a subject that will be discussed further in Chapter 11.

"Choosey female, indiscriminate male" is of course a bit of a caricature, although it reflects a real asymmetry. Individual sperm are indeed cheap, but whole ejaculates may not be [152], especially when they constitute a nutrient-rich "nuptial gift," as we shall see. And where males make a major parental contribution, as in most birds, a misingrate can be as much a disaster for males as for females. In such cases, males have to be a little choosey too [289]. Males also have to be somewhat selective when there is a significant time cost of mating. In isopods, for example, an order of invertebrates including sowbugs, males often guard females from other males for several days before mating, actually carrying the female about until she is ready to copulate. The males are then selective, preferring to guard larger females who will produce larger numbers of eggs [413, 567]. But it is precisely because the female is so often the scarce resource, valued and fought over by males, that she is frequently in a position to be more choosey and to demand that her suitors assume at least some of the costs of the reproductive enterprise.

FEMALE CHOICE: MAKING THE MALES PAY

The black-tipped hangingfly is a slender predatory insect that hunts in the dense low foliage of temperate forests. Its prey consists of houseflies, aphids, daddy longlegs, and other small animals of the forest floor; and according to Randy Thornhill of the University of New Mexico [605], female hangingflies prey upon arthropods of various sizes in proportion to their abundance. Not so the males. When a male hangingfly catches a dead arthropod, he feeds on it only briefly and then does one of two things. A small prey item he discards to look for another. But if the prey item is a certain threshold size, the male everts a pair of abdominal glands and lets a special chemical waft away on the breeze, the advertisement of a successful hunter.

The target of the male's chemical signal is of course a female, and when she approaches, the male passes her the prey item (without relinquishing his hold on it!) and attempts to mate while she feeds (Figure 6-1). If the prey item is inadequate, she breaks off copulation before any sperm are transferred and departs. If it's a big juicy fly, on the other hand, she will permit copulation to continue for the full twenty minutes necessary for complete sperm transfer. Once that goal has been attained, the male becomes increasingly likely to break off copulation and snatch back his gift,

FIGURE 6-1
Hangingflies, *Hylobittacus apicalis*.



During copulation, the female is feeding on a prey item brought by the male.
(Photograph by R. Thornhill.)

which may still be good enough to win him another female! Meanwhile, his mate ignores advertising males for about four hours and goes off to lay about three eggs. Her egg production is to some degree a function of the size of the nuptial gift. Males are quite clearly buying fertilizations.

The female hangingfly seems to have taken control of the mating system, and she lets the male serve her. When things are going well, she hardly has to hunt at all. Hunting is dangerous for these animals, for as they move through the foliage in search of prey, they frequently run afoul of their major source of mortality—web-building spiders. And it is males, who travel about twice as far as females, who mostly get snagged.

So females with their precious ova are not quite such helpless victims of roving males as might be imagined. They have their ways of making males pay. Thornhill [606] has reviewed a fascinating range of such transactions among the insects. In some species the male must provide a proteinaceous spermatophore, which the female assimilates, if his sperm is to be accepted. The spermatophore may weigh up to a quarter of his body weight. In some flies, grasshoppers, and other insects, females feed upon glandular secretions from the male during copulation; if he stops secreting,

she stops mating. Finally, it is not rare for the male himself to be consumed by his mate.

Nuptial feeding is even more conspicuous in birds. Ornithologists have long been aware that males feed females in courtship and during nesting, but until recently little attention was paid to the energetic value of the gift. Courtship feeding turns out to be no arbitrary ritual [536]. Terns, for example, are colonially nesting birds who plunge-dive for fish and shrimp. In a fine study of common terns by Ian Nisbet of the Massachusetts Audubon Society [461], it was found that the rate at which males feed their mates is maximal just when the energetic cost of egg production is maximal. Even more interesting was the fact that pairs varied in their nuptial feeding rates, and that the rate at which the male fed his mate was predictive of the weight of her clutch.

In Chapter 5 we discussed some cases in which males can use two or more alternative mating strategies (pp. 103–104). In such a case, the females may prefer the male strategy that is most profitable for them, discriminating against the alternatives. This is very clearly the situation in scorpionflies (*Panorpa*), who are close relatives of the hangingflies and, like them, have been studied by Randy Thornhill [607, 608]. Like hangingflies, *Panorpa* suitors acquire a dead arthropod, emit a pheromone to attract a female, and present it to her as a “nuptial gift.” But when they cannot get a suitable prey item, male scorpionflies switch tactics. They secrete a salivary mass and advertise for a female in the same way they would with a prey. Male salivary glands are enormous—perhaps a quarter of the insect’s total weight—and their secretion is nutritious. So a male with no other nuptial gift to offer gives the female of himself. And there is a third avenue—rape. With neither a nuptial gift nor a secretion of pheromone, the male may simply try to knock a passing female out of the air, immobilize her with specialized claspers and clamps, and inseminate her forcefully. Males prefer the arthropod ploy—if you give them an arthropod, they’ll use it and forsake the alternatives. Without a prey, they’ll use saliva if they can afford it. Rape seems to be a last resort. That the males would prefer to use a prey item rather than their own saliva is not surprising, since salivary secretion is debilitating. But it is less obvious why both advertising strategies are preferred over rape. It appears that this priority is female-enforced. Females flee from and resist males who attempt to use force, and they manage to escape about 85 percent of the time. They have a further line of defense too. In the laboratory, Thornhill found that insemination was successful in all “honest” resource-transfer copulations, but was somehow blocked as often as not if the female had been raped. By discriminating against rapists, then, female scorpionflies selectively maintain a style of male courtship that offers them some material gain and some choice in who will inseminate them.

In a few cases, the resources that male insects provide to females are

so substantial that the male has evidently become a limiting resource for female reproduction, rather than the reverse. In the Mormon cricket (actually a katydid), for example, the male provides a proteinaceous spermatophore equal to 20 percent of his body weight. Unlike other katydid species with smaller spermatophores, female Mormon crickets fight over males, and males are coy and choosey [237]. We shall return to the subject of "sex-role reversal" in Chapter 7.

RESOURCE-DEFENSE POLYGYNY

A male can achieve some degree of polygynous monopoly by aggressively guarding several females. It's an exhausting strategy, and as we saw in the bison, a total monopoly is often not attainable, but female defense by a dominant male can certainly pay off in a better-than-average number of fertilizations.

But what if the females won't stick together? Simply being the toughest male around may not be much help. As we have seen, males may switch to scramble competition when the females are not defensible. There is also a third possibility: Though the male may be unable to herd and control the females, he can set up a territory in some place that females are sure to come to, and he can exclude other males. A steadily producing food source that will regularly attract mobile females may be worth defending. Hummingbirds, for example, feed on nectar, and a flowering bush may be guarded by a male who excludes other males while permitting females to feed in exchange for copulations [691]. This is rather like the hangingfly's nuptial gift, except that the nectar source is stationary, and the male has no other claim to it than his ability to exclude others. In many insects, amphibians, and fish, ideal sites for oviposition or spawning are limited and are defended by large, relatively successful males who are able to keep their rivals at bay and fertilize the eggs of multiple females. Finally, where there is post-zygotic care, as in all birds and mammals, females often establish their separate breeding sites close enough together for males to attempt to defend exclusive territories encompassing two or more breeding females. It is this latter sort of territorial polygyny that we should like to examine in a little more depth.

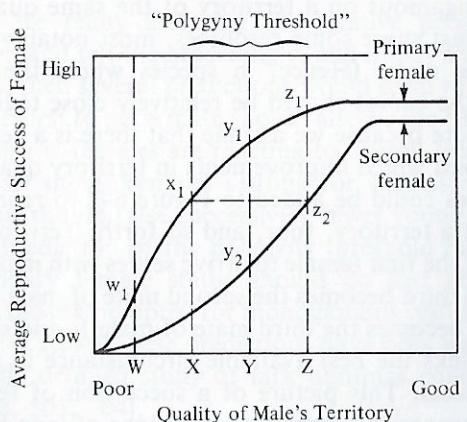
THE POLYGYNY THRESHOLD

Most migratory songbirds—robins and warblers and finches and so forth—are predominantly monogamous. A male establishes a territory, attracts a single mate, and shares parental duties with her over the nesting cycle. But a

minority of species—the ubiquitous red-winged blackbird of North America is one example—are regularly polygynous. Individual males are commonly able to attract two or three or four or more females to nest within their territories. Why? It would seem, from the arguments developed earlier, that males of *any* species might strive to accumulate multiple mates. If there is always an advantage to polygyny for the male, and yet it does not always occur, then the circumstances under which it does occur must be those in which there is also some advantage for the female. This, at least, is the argument advanced by Gordon Orians in an attempt to explain the diversity of mating systems [473]. He elaborated upon the earlier ideas of Verner and Willson [642], who coined the term "polygyny threshold."

This concept is best explained with reference to migratory songbirds.

FIGURE 6-2
The Orians-Verner-Willson "polygyny threshold"



Male territories vary in quality in such a way that females tend to enjoy greater reproductive success on a "good" territory than on a "poor" one. Males arrive first and set up territories. Imagine, for example, that four males have territories of quality *W*, *X*, *Y*, and *Z*. Females then arrive and evaluate the territories. The first female should choose the territory of quality *Z* and thus enjoy reproductive success *z*₁. The second should opt for *Y* and *y*₁. But the third female can do as well by being the second mate on the *Z* territory or monogamous on the *X* territory: *z*₂ = *x*₁ and the difference in territory qualities has reached the "polygyny threshold." The territory of quality *W* is so poor that females would do better to be bigamously mated on either *Z* or *Y*. The male there may remain a bachelor, while the males on *Z* and *Y* each have two mates and the male on *X* has one. (After Verner & Willson, 1966 [642] Copyright © 1966 by the Ecological Society of America; Orians, 1969 [473].)

Males arrive upon the breeding grounds in the spring before the females, and begin to sort out territories among themselves. Some males get choice territories, while others settle for poor ones. When the females arrive, each settles on the best available territory for nesting; in so doing, she incidentally picks a mate (though to what extent females may be influenced by the male himself is still unresolved; see p. 128). The consequences of variation in the quality of the territories are illustrated in Figure 6-2. Where the difference between the qualities of available territories exceeds the polygyny threshold, as shown in the figure, a female will do better as a second mate on a good territory than as a first mate on a bad one. What makes a territory good or bad varies with the species in question and with the ecological circumstances. It might be the availability of suitable nest sites or materials, of food for the nestlings, or of good conditions for the detection of approaching predators. What is crucial is that territory quality varies in some way that the female can assess.

The two curves in Figure 6-2 represent the cases of monogamy and bigamy. We assume that a female will fledge fewer young when bigamous than when monogamous on a territory of the same quality because bigamous females must share some resources, most notably the parental contributions of the male. (Hence, in species where the male contributes relatively little, the curves should be relatively close together.) The curves reach an asymptote because we assume that there is a ceiling on reproductive success beyond which improvements in territory quality are irrelevant.

Other curves could be added to Figure 6-2 to represent the cases of three females on a territory, four, and so forth. Territory qualities might then be such that the first female to arrive settles with male 1 and the second with male 2. The third becomes the second mate of male 1, the fourth joins male 3, the fifth becomes the third mate of male 1, and so forth. Each successive female picks the best available circumstance in terms of expected reproductive success. This picture of a succession of female arrivals and choices is consistent with Verner's observations of long-billed marsh wrens and with Orians's and Willson's of blackbirds.

According to the polygyny threshold model, monogamy should result when the curves are relatively flat (and/or relatively far apart) over the range of existing territories. More plainly, monogamy is expected where territory quality does not vary greatly, so that each arriving female will do better to accept the best remaining bachelor territory than to accept second female status on a slightly better one. This suggests that those species of migratory songbirds that are regularly monogamous are not irrevocably so but practice monogamy in response to particular ecological circumstances. This suggestion gains some plausibility from observations of occasional polygyny in a large number of species that are usually monogamous.

Is polygyny in fact prevalent in those species where the variance in male territory quality is especially large? Measurement of territory quality is difficult, but there is some relevant evidence at a broad level of comparison. Ecological data suggest that marshes, which contain lush patches distributed irregularly according to water depth and other variables, should be habitats with especially great diversity in territory quality. According to Verner and Willson [642], only 14 of the 291 species of songbirds nesting in North America are regularly polygynous and only 18 are marsh nesters or marsh feeders during nesting, yet there are 8 species of polygynous marsh users. Polygyny is therefore far more prevalent among marsh users (44 percent) than among other songbirds (2 percent). This correlation is very impressive. However, in Europe, ornithologists have not found polygyny to be especially prevalent among marsh nesters. The polygyny threshold argument, that polygyny will occur where there is great variance in territory quality, may still be applicable to the polygynous birds of Europe, with the availability of suitable nest sites being the crucial and highly variable aspect of territory quality [238, 686].

If females are really assessing the relative promise of available breeding situations and settling accordingly, and if they are at all accurate in these assessments, then several predictions would seem to follow. The same males who are the first to get a mate should also be the first to get a second and a third (at least if females are reacting to overall territory quality and not to specific nest sites). Females settling for successively less preferred breeding situations should raise successively fewer young. And perhaps the most interesting prediction of the polygyny threshold model is that those opting for secondary female status should do just about equally well reproductively as those who opted for monogamous status *at the same time*; in Figure 6-2, $x_1 = z_2$. All these predictions have been neatly corroborated in an exceptionally detailed study of lark buntings conducted by Wanda Pleszczynska [208, 503, 504].

In the grassy Great Plains of North America the dramatic black-and-white male lark buntings make sure their presence is known, while the females are inconspicuous. (After marshes, grasslands seem to be the habitat where songbirds are most often polygynous.) A rare virtue of Pleszczynska's study was that she was able to identify a simple measure of territory quality that proved to be highly predictive of both female preference and reproductive success. That measure was shade, for it seems that a shady nest site on the treeless plains is a precious commodity. Having observed that shade was related to female choice and to fitness, Pleszczynska verified that the relationships were causal by adding plastic rosettes of leaves to alfalfa plants in some territories; the effect was both to increase fledging success and to enable the lucky males on those territories to attract

three females, something that never occurred in the absence of experimental intervention! Male lark buntings, like so many other species, get their territories sorted out before the arrival of the females. By intensive observation during the two-week period of initial female arrivals, Pleszczynska was then able to confirm each of her predictions (Figure 6-3).

In those highly polygynous songbird species in which the male does not participate in parental care, our emphasis may be somewhat misplaced when we speak of females opting for a polygynous or monogamous breeding situation. In some populations of red-winged blackbirds, for example, males are never observed to feed young. The female's choice may simply be a matter of the best available nest site, with the male's mating status and territorial boundaries largely irrelevant to her. In fact, the local territorial male may not even be the sire of all her young, although he probably sires most of them [65]. But where the male contributes to the young, the female should be more concerned with the distinction between being monogamously mated or polygynously mated.

FIGURE 6-3
Polygyny in the lark bunting

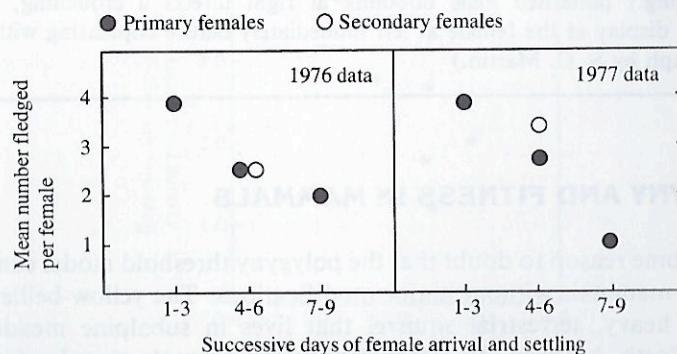
Table entries indicate when each male acquired first, second, third mate

		1977 data									1978 data										
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Male's territory quality, ranked according to available shade	Most shade	1			2		3														
	Least shade	2	1		2		3														
		3	1		2		3														
		4	1			2															
		5	1			2															
		6	1			2															
		7	1			2															
		8	1				2														
		9		1																	
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		16								1											
		17									1										
		18										1									
		19											1								
		20																			
		1	2	3	4	5	6	7	8	9	10	11	12	1	2	3	4	5	6	7	
		Successive days of female arrival and settling																			

In several species of polygynous songbirds the male helps his first female feed her brood but leaves any subsequent mates to fend for themselves [e.g., 485]. Even so, a female may choose to become mate number 2 on a fine territory while territorial bachelors are still available. An example is the bobolink (*Dolichonyx oryzivorus*, Figure 6-4), a regularly polygynous bird of North American pastures and cropfields that is in many ways reminiscent of the lark bunting. In a careful long-term study, Stephen Martin found that the unaided second female had decidedly less reproductive success than the assisted first female [414]. Second females laid 4.8 eggs per clutch and successfully fledged young from 49 percent of their eggs; the comparable figures for first females were 5.5 and 64 percent, respectively. The lower success rate of the second females was clearly due to their lesser ability to feed the nestlings without male assistance. That females continue to choose this second-female status over mating with remaining bachelors suggests that their reduced payoff must still exceed what they could hope for on the poorer territories, even with male help.

Females behave in accordance with the polygyny threshold model, successively occupying territories according to their quality, and choosing polygynous status on the best territories in preference to monogamy on the worst.

Moreover, reproductive success is maximal for those females choosing first, and declines with successively less preferred breeding situations. Monogamous and bigamous females settling at about the same time do about equally well.



(After Pleszczynska & Hansell, 1980, Tables 2 and 3 © 1980 by the University of Chicago [504]; Garson, Pleszczynska & Holm 1981, Table 1 [208].)

FIGURE 6-4

The strikingly patterned male bobolink at right directs a crouching, wing-spreading display at the female at left immediately before copulating with her. (Photograph by S. G. Martin.)

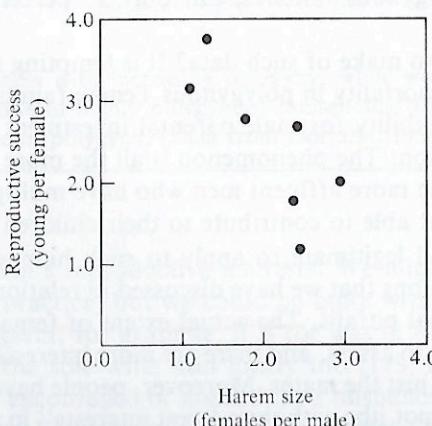
POLYGYNY AND FITNESS IN MAMMALS

There is some reason to doubt that the polygyny threshold model can be extended to mammals without major modifications. The yellow-bellied marmot is a heavy, terrestrial squirrel that lives in subalpine meadows in western North America. In suitable habitat, marmots may be found in concentrations ("colonies"), but the species is only moderately sociable. According to a study by Downhower and Armitage [164], adult males are territorial and mutually antagonistic. The territory that a male defends en-

compasses one to four breeding females. As we would expect, a male's reproductive output, measured by the number of yearlings produced, increases with harem size. However, female reproductive success declines sharply as harem size increases (Figure 6-5). Downhower and Armitage interpreted their results as contrary to Orians's notion that polygyny occurs because of its advantages to females. Monogamy is clearly the best mating system from the point of view of the female yellow-bellied marmot, yet polygyny exists. The usual harem size of two is a compromise, they suggested, between the still more polygynous inclinations of the male and the female's preference for monogamy.

The argument has been criticized by Elliott, who doubts whether the large-harem female suffers reduced fitness [177]. The loss of fitness may not be shared equally among all females. There is a dominance hierarchy among the females, and the senior female is not necessarily harmed by the presence of the others. So it may be only the young females that do worse in big harems than they would in a monogamous situation. Their present loss may be compensated by improved survival prospects, resulting from the predator-detection advantages the larger harems enjoy in comparison to more isolated smaller groups. Elliott still favors the notion that polygyny

FIGURE 6-5
*Harem size and reproductive success in the yellow-bellied marmot, *Marmota flaviventris**



Females in larger harems produce fewer surviving young. (After Downhower & Armitage, 1971 [164].)

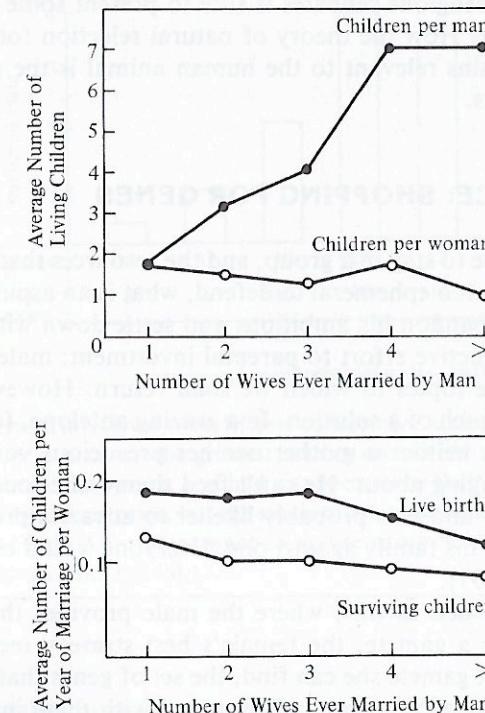
must serve the female in order for it to have evolved. Nevertheless, the polygyny threshold theory is decidedly less compelling in mammals than in migratory songbirds. A terrestrial rodent like the marmot does not have the mobility to visit all available male territories and thus make an informed choice. Moreover, in some harem-forming mammals male coercion clearly limits female choice. We have already described the male Hamadryas baboon that herds his females and punishes those who stray, and there are a number of hoofed mammals that behave similarly. As Downhower and Armitage quite rightly stress, the optimal reproductive strategies of a male and female are not perfectly harmonious, and there is no reason to suppose that either mate will be able to achieve its own optimum in conflict with the other. The concept of a conflict of interests between mates will be developed further in the next chapter.

The available human data on polygyny and reproductive success are reminiscent of the marmot findings: Polygyny costs the female and benefits the male. Among the Temne people of Sierra Leone, for example, anthropologist Vernon Dorjahn found 54 percent of 246 married men to be polygynous [161]. Men gained in fitness from increasing degrees of polygyny, while women lost (Figure 6-6). The decline in female fertility may appear to be small, but it is statistically reliable and by no means trivial. Figure 6-6 shows that the reproductive loss in polygynous women has two separable components. The rate of live births declines, but only after the man has four or more wives. Infant mortality becomes a factor sooner. It is higher at all levels of polygyny than in monogamous marriages—41 percent of children born to bigamous households died, an identical proportion in the still more polygynous families, but only 25 percent in monogamous households.

What are we to make of such data? It is tempting to suppose that the heightened infant mortality in polygynous Temne families is somehow due to the reduced possibility for male parental investment in each offspring, but this is speculation. The phenomenon is all the more striking in view of the fact that it is the more affluent men who have multiple wives, and they are presumably best able to contribute to their children's welfare.

But is it at all legitimate to apply to such human data the kind of strategic considerations that we have discussed in relation to other animals? There are substantial pitfalls. The actual extent of female choice and male coercion is difficult to assess, and there are more interested parties in a marriage contract than just the mates. Moreover, people have expressible intentions that often do not jibe with their "best interests" in terms of biological fitness. And their actual behavior may accord with neither! We shall discuss this further in Chapter 11, but for the moment an example will suffice. It would seem from the Temne study and other similar data that polygyny is

FIGURE 6-6
Polygyny and reproductive success in Temne people



(a) Men gain in fitness with increasing polygyny, while women lose. (b) Live births per wife decline in highly polygynous households. Infant survival is reduced by any degree of polygyny. (Data from Dorjahn, 1958 [161].)

contrary to a woman's reproductive interests. We might suppose that she should dislike the practice, but we could be quite wrong. Among the Ibo and Yoruba of Nigeria, for example, it is (or was in recent times) slightly humiliating to be the sole wife, and lonely too [173, 650]. Monogamous women commonly encouraged or goaded their husbands to marry again. It seems that a form of Elliott's argument applies here: The reproductive success of a senior wife is apparently not compromised by polygyny, which might even serve her interests by bringing in a helper [309, 628]. But we should not be greatly surprised to discover, in any particular case such as

this, that fitness is decidedly not maximized. People limit their reproduction in a multitude of ways, both deliberate and incidental to other goals. Any species that includes substantial numbers of childless couples, exclusive homosexuals, and religious celibates is sure to present some complications for the evolutionist! How the theory of natural selection for reproduction maximization remains relevant to the human animal is the subject of our concluding chapters.

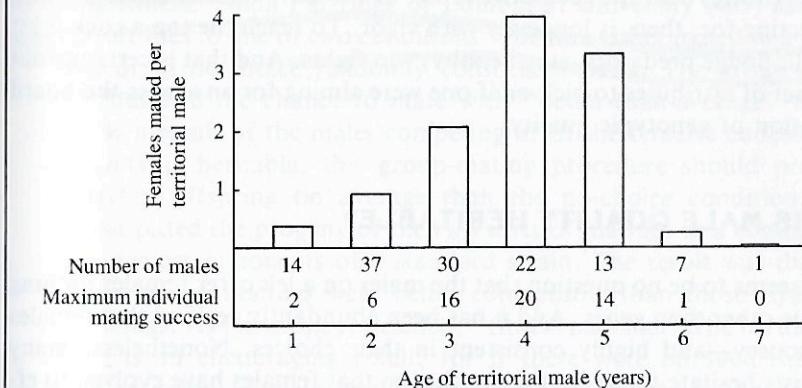
FEMALE CHOICE: SHOPPING FOR GENES

If the females refuse to stay in a group, and the resources that females value are too scattered or too ephemeral to defend, what is an aspiring polygynist to do? He might abandon his ambitions and settle down with one female, reallocating reproductive effort to parental investment; male parental care and monogamy are topics to which we shall return. However, this often doesn't seem like much of a solution. In a grazing antelope, for example, or a browsing grouse, neither a mother nor her precocious young has much need of a male hanging about. He can't feed them—the food doesn't lend itself to gathering—and he's probably likelier to attract a predator than to successfully defend his family against one. Everyone would be happier if he would just leave [697].

In situations such as this, where the male provides the female with nothing other than a gamete, the female's best strategy seems clear. She should pick the best gamete she can find, the set of genes that will best contribute to the fitness of *her* genes when united with them in an offspring. And this female strategy suggests what a male must do: propagandize. Without so much as a nuptial gift, the male's plight is like an old song lyric: "All I have to offer you is me." It's up to the singer to make that offer appear attractive, *more* attractive in fact than the same offer being sung by every other male in the vicinity.

Whether females actually assess male genetic quality in choosing mates has troubled field biologists and theorists for decades. In territorial, polygynous birds such as the red-winged blackbird, many workers have tried to discover whether female choice is affected by both the territory and the male or just by the territory alone. This is not an easy question to settle. The best males will generally hold the best territories, so one must somehow eliminate the correlation between the two factors if one is to separate their effects. Experimental approaches are not necessarily successful, since the animals may respond by changing positions or boundaries and reestablishing the correlation. There are some complex arguments in favor of the hypothesis that male quality is not altogether ignored [655, 701], but the ef-

FIGURE 6-7
Effect of age on mating success in male black grouse



On a lek observed intensively for fifteen consecutive spring breeding seasons, four-year-old cocks attained the greatest mating success. Most males first held a territory in their second spring, and had disappeared by their fifth. In an average year, 9.6 males held territories, but the single most successful male got 54 percent of the matings. Only 3.6 percent went to non-territory-holders. (After De Vos, 1983, Appendices 2 and 3 [146].)

fect of male quality upon female choice in resource-defense systems is still unresolved.

Where the male offers nothing but himself—that is to say his genes—the situation seems clearer. And the clearest such mating system is that referred to by the Swedish label **lek**. Males congregate at a fixed site, the lek, and display en masse while defending a small area each from the others. Lek sites commonly persist for many years. Females visit the lek, peruse the selection of strenuously posturing males, and choose in whose territory they will tarry and be mated. Leks are used only for mating. No feeding occurs there, and the females depart quickly once serviced. These communal display grounds may be conspicuous at great distances as a result of the spectacular displays of the assembled males. Lek systems occur sporadically in several bird families and in a few mammals, fish, and insects.

In lek-breeding grouse [146], it has been demonstrated that the preferred males are the oldest. A young cock must attend the lek for years with little or no sexual reward before he can move up to the status of a successful breeder (Figure 6-7). Each time one of the more central cocks disappears,

the younger, more subordinate, more peripheral cocks jockey about to move in a notch toward the charmed inner circle. (In other lek-breeding birds, such as manakins, the most successful males do not necessarily occupy territories near the geometric center of the lek.) What the hens seem to be selecting for, then, is longevity with vigor. To reach the top a cock must eat well, dodge predators, stay healthy, win fights. And that is certainly not a bad set of attributes to pick on if one were aiming for an across-the-board evaluation of genotypic quality.

BUT IS MALE QUALITY HERITABLE?

There seems to be no question that the males on a lek offer females nothing of value other than genes. And it has been abundantly verified that females are choosy—and highly consistent in their choices. Nonetheless, many biologists hesitate to accept the conclusion that females have evolved to effectively select the best male genotype. The argument against the gene-shopping interpretation of mate selection is a theoretical one. The lek mating system is one where the variance in male reproductive success is large [e.g., 272, 347, 673]; visiting females evidently select males upon consistent criteria, so that a few preferred males get a huge proportion of all copulations. Now, if *every* male is the offspring of a genetically superior father, then surely inferior genotypes must be rapidly eliminated by selection. Recall that any trait that has been subject to selection is likely to have a low heritability (p. 33). How, then, can fitness itself be heritable? It would seem that the males on a lek are unlikely to vary much in their genetic fitness potential. According to this argument, variation in fitness must, for the most part, be environmentally induced, especially in highly polygamous mating systems, and if that is so, then females cannot use phenotypic cues to shop for good genes.

This objection has been raised by many leading theorists, but it can be countered both theoretically and empirically. The idea that fitness variations must have only a minor heritable component is based on population genetic models with additive fitness effects of the genes at each of several loci. Such models are indubitably oversimplified. As soon as one considers that particular *combinations* of genes may have nonadditive fitness benefits, important genetic differences between males on the lek become feasible. And possibly even more important is the organism's overall level of heterozygosity across *all* genetic loci. Considerable variability in individual degrees of heterozygosity is to be expected, and there is evidence that high levels of heterozygosity contribute to fitness; if a female wishes to maximize heterozygosity in her offspring, she should mate with the most heterozygous male available [61]. By choosing the oldest, most vigorous, or

most dominant male on a lek, then, females may simply be managing the breeding system to maximize offspring heterozygosity.

A recent experiment confirms that selective mating can contribute to offspring fitness. Linda Partridge of Edinburgh University [483] assigned female fruit flies to one of two conditions. The flies either mated in a group situation or in no-choice randomly constituted pairs. The group-mated females thus had the chance to mate with “better-than-average” males, whether as a result of the males competing or of the females choosing. If male quality is heritable, this group-mating procedure should produce better-quality offspring on average than the no-choice condition. The critical test pitted the progeny of the two sorts of matings in a competitive situation against opponents of a standard strain. The result was that the progeny of group matings were better competitors than those from no-choice matings. As Partridge concluded, “fitness may indeed be heritable.” And that is an encouraging result, for if there were no such thing as heritable variation in male quality, then female choice, at the lek and elsewhere, would seem a meaningless charade.

RUNAWAY SEXUAL SELECTION

When Darwin first theorized that certain sexually dimorphic characters might be “sexually selected,” he drew a distinction between those characters of service in competition between individuals of the same sex (usually male) and those which served to attract members of the opposite sex (usually female). He remarked, however, that the same character—such as horns or other male armaments—might be effective in both contexts, and this is probably the general case. Effects of certain male attributes upon male-male competitive success and upon female choice have been demonstrated empirically, but an intriguing question remains unresolved: Are any of the traits that we observe utterly arbitrary products of a “runaway process” of preferential mate choice? As Sir Ronald Fisher [191] pointed out, preferential mate choice has a peculiar capacity to be self-reinforcing. If some females find some arbitrary characteristic attractive—orange hair, say—then a rare orange-haired male will be on average a little fitter by virtue of this little attractiveness edge, all else equal. Well, as soon as there is a selective advantage to orange hair, there is immediately instituted a selective advantage for those who *prefer* it, since such females are likelier to have orange-haired sons who will enjoy the fitness benefits of . . . and so on. A sort of bandwagon effect ensues; nobody wants to be left out: Once most females prefer orange hair, the sons of any female who does *not* conform are likely to be losers. Fisher felt that a runaway process of this sort was necessary to account for such “extravagant” display features as the cock

pheasant's tail, and he verified that such a process was feasible with population genetic models.

Fisher's formal analysis has been widely accepted and elaborated upon, but many biologists question the importance of runaway sexual selection in nature. If there are "real" differences in genetic quality between the males that court a female, then fancying orange hair would seem rather frivolous. "Extravagant" display characteristics are furthermore not just arbitrary differences like orange versus green hair—they are positively costly! The flight and foraging abilities of males who drag great plumes behind them are compromised. Mightn't there be something more to this than runaway sexual selection? In 1975, Amotz Zahavi, a voluble Israeli biologist, suggested that the costliness of extravagant characteristics is precisely their point: They are "handicaps" that are displayed to advertise their bearer's capacity to endure them [706].

Zahavi argues his perspective in an informal, anthropomorphic style. A male with a huge tail, he suggests, is transmitting a message: "Look at the burden I bear! Can you doubt that I must be exceptionally nimble in avoiding predators, and skilled in gathering food, if I can afford to divert resources into such an absurd impediment?" Reaction to this argument has been mostly critical—even hostile—but that reaction seems to be due more to its style than to its content. Zahavi disdains formal models, and his flamboyant translations of the messages in animal displays are easy targets for nit-picking. Several population geneticists have responded by constructing models in which a "handicap gene"—a mutant allele imposing a handicap and hence a fitness cost on its bearer—cannot spread by sexual selection. One leading theorist has set the handicap theory on the shelf with this declaration: "I see little point in further discussion until it has been shown to work in at least one plausible genetic model" [424, p. 174]. It is not altogether clear, however, that the genetic modelers approached Zahavi's argument in the right spirit. The "handicap" is probably not best conceived as an inevitable fitness penalty. It is a burdensome trait that is expressed only in those individuals who can "afford" it [707]: "Look at the size of my antlers. I must be very vigorous to be able to support them." When the handicap principle is modeled in this way, then it is indeed plausible [181].

HONEST ADVERTISING

The point that Zahavi has been making is in fact more general than we have yet indicated. It is that signal systems tend to evolve toward "truth in advertising." Suppose, for example, that females are concerned to choose the male of the best genetic quality. Any phenotypic indicator of male quality that they use to make that choice should be a valid one, or else females will

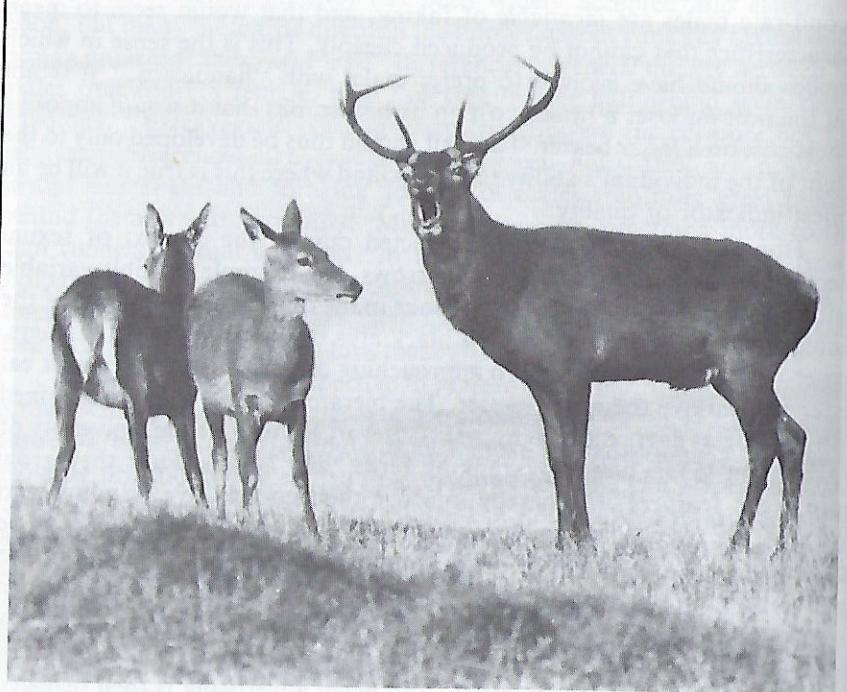
be selected to ignore it. What is to keep a second-rate male from "faking" high quality? Females must choose on the basis of characteristics that second-rate males are *incapable* of faking, and that would seem to mean characteristics that cannot be produced cheaply. This is the sense in which females should have evolved to prefer males with "handicaps." It is not that the trait imposes a fitness cost on its bearer, but that it *would* impose a fitness cost on a *lesser* bearer. The trait should thus be developed only to the extent of the individual's ability to bear it, and where this is true it will be an honest indicator of quality.

Honest advertising is to be expected outside the context of sexual selection too [e.g., 505]. Harris's sparrows, for example, exhibit variable winter plumages—the higher a bird ranks in the dominance hierarchy of the winter feeding flock, the larger is a black area of breast and head feathers. Lower-ranking birds give way to approaching dark birds, and the latter eat better and survive the winter better. The hierarchy seems to be maintained with little overt aggression. Why, asked Sievert Rohwer of the University of Washington [533], don't low-ranking birds "lie"? Why don't they grow more black feathers and thereby improve their competitive standing? To find out, he dyed some low-ranking birds so that they appeared to be dominants, and you may have guessed the outcome. The dye job didn't do them any good. The impostors were unable to make good on the bluff when they were aggressively challenged. The dominance hierarchy is generally maintained without *much* overt aggression, but the relative rank of birds of similar status is occasionally tested. And when advertising is then revealed to be false, the aggression persists and intensifies. Honesty seems to be the best policy for a Harris's sparrow.

Mate attraction displays ought to be similarly unfakable. Female toads, for example, have been shown to be attracted to the deep croaks of the largest males. The pitch of a croak is determined by the dimensions of the sound producer in such a way that small males are simply incapable of mimicking big males' voices [139]. An almost identical circumstance has been demonstrated in the red deer [105]. The hinds are attracted to the loudest, longest roars, and the volume and duration of a stag's roar are limited by his chest capacity (Figure 6-8).

It is again the lek mating system where the effects of female choice ought to be clearest—undiluted by male defense of either females themselves or the resources that females value. When males strut and puff in front of a critical audience of potential inseminees, we must assume that it is the females who have selected, over evolutionary time, for the strutting and puffing. Why? It seems unlikely that females find malicious fun in making males look ridiculous! In a variant of honest-advertising theory that he calls the "war propaganda" model, Gerry Borgia [61] has argued that females insist that males on leks—and indeed territorial males in general—put on

FIGURE 6-8
Red deer: stag with hinds.



(Photograph by T. H. Clutton-Brock.)

conspicuous displays in order to test the veracity of their claims to dominance. The point is that displays attract the attention of rival males as well as females, so that any male who has not established his dominance rank fairly through a history of male-male interactions will be challenged and found out.

A clear example of just this sort of enforcement of honest advertising is provided by some outstanding studies of brown-headed cowbirds by Meredith West and Andrew King [660]. In these brood-parasitic birds, females are induced to solicit copulation by male song. Dominant males sing more potent songs than subordinates, and one is immediately led to wonder why anyone would sing a relatively ineffective song. The answer has been provided by experiment. It is his competitors who ensure that a male's song reflects his true status. Isolate a male and his song will change over time to a dominant, potent one. But return him to a competitive situation and the other males will attack him whenever he sings, although they will

not attack an equally strange male if he sings a subordinate, ineffective song. Like the Harris's sparrow, the cowbird who advertises falsely is persecuted mercilessly.

An idea similar to the "war propaganda" model was advanced for elephant seals by Cathy Cox and Burney LeBoeuf, although in this case the female herself loudly draws attention to any male who may be bluffing high status [117, 118]. When a bull seal mounts an estrous female to attempt copulation, she makes such a fuss that other bulls are attracted to challenge him, and it is then the most dominant male who generally ends up with the copulation. Cox and LeBoeuf called this "female incitation of male-male competition" and the parallel to Borgia's "war propaganda" model should be clear: Although in the one case it is the female and in the other the male who raises the attention-getting ruckus, in both cases it is ultimately the females who are really insisting that the males' status be confirmed.

Whatever one may think of the concept of "handicaps," then, Zahavi has drawn attention to a fundamental aspect of animal social behavior. Individuals are always striving to manipulate one another to their own fitness advantage, and propaganda should therefore be tested before it is believed. Fakable information is no information at all. Communication systems are likely to evolve in the direction of honest advertising, not because honesty is a virtue, but because chronic lies and uninformative signals will come to be devalued and ignored.

SUMMARY

Females are generally more selective in mating than are males, as is to be expected since a mismatch can cost a female much wasted nurture and lost reproductive potential.

Females sometimes demand nuptial gifts from males in exchange for fertilizations, and they sometimes choose mates on the basis of territory quality. In some cases, such as lek systems, females apparently select a mate for the quality of his genes.

Females selecting mates, and indeed animals responding to any sort of social signals, should evolve to attend only to those aspects of signals that cannot easily be faked and are therefore truly informative.

SUGGESTED READINGS

- Borgia, G. 1979. Sexual selection and the evolution of mating systems. In M. S. Blum & N. A. Blum, eds. *Sexual selection and reproductive competition in insects*. New York: Academic Press.