to masculine females, as another case of gender meshing. Alternatively, they may have a role in facilitating courtship. Also, mating in some of the species takes place in leks, suggesting a comparison to the feminine male sunfish and ruffs found in leks. Perhaps the feminine males have a role in facilitating courtship at the leks. In any case, the data on museum specimens show that transgender expression is widespread in hummingbirds, inviting follow-up fieldwork.

For a case of transgendered behavior, let us turn to the opposite extreme in data collection, a single individual in the field. Hooded warblers *(Wilsonia cirtina)* live in woods of the mid-Atlantic United States. They are named for the black plumage that adult males have on their heads—a hood. Some females also have these black hoods, and can't be distinguished from males by birdwatchers.[41] Early on, variation in female plumage color was thought to represent age, but later work showed that the color is permanent, suggesting a genetic polymorphism for color. About 5 percent of the females very closely resemble males.

Of particular interest is one transgendered black-hooded warbler that was discovered in Maryland.[42] The bird was originally assumed to be a masculine female, but was later discovered to be gonadally male. Black-hooded warblers are monogamous, and the transgendered bird behaved as the female member of a monogamous pair, consistently showing female-typical behavior throughout two years, including nest building, incubating and brooding young, and not singing or engaging in territorial defense. The bodily appearance of the transgendered bird was typical of males, the behavior typical of females. This bird pair-bonded to a male who was also typically male in both appearance and behavior.[43] In this case, a male-bodied bird behaved in all respects like a female, except for laying eggs. Gender identity in this individual hooded warbler evidently crossed over from that typical of the sexed body.

In conclusion, families with multiple genders can be explained using the concepts developed for two-gender families. The idea of helping at the nest in return for reproductive access that was devised for social insects and applied to extended families of birds and mammals also works for how multiple genders are integrated into a social system. Extending kin

selection theory now leads to a theory for a labor market that trades access to reproductive opportunity for service, with genetic relationship merely affecting the worth of a unit of reproductive access. The different genders represent different sectors within this economy. While some sectors, like the end-runners, clearly compete with the controllers, others (like the cooperators) are service providers working under contract. Understanding this complex and interesting social dynamic, an animal political economy, I believe is the next step for evolutionary social theory. The part of Darwin's theory of sexual selection that predicts universal male and female templates may be false, but an evolutionary approach to social behavior is alive and well.

7

Female Choice

As further evidence of the difficulties with sexual selection theory, let's consider how real-life female choice differs from female choice in Darwin's sexual selection theory. Darwin focuses on mating only. A female is supposed to select males according to their attractiveness and prowess. Males are supposed to compete among themselves for mating opportunities and to advertise their good looks to females. This peculiar emphasis on the mating act alone is simply not supported by actual female choices, which are more concerned with the totality of reproduction, including the growth and protection of the young.

"Darwinian fitness" is a technical term that refers to production of the young who will partake in the next generation's reproduction; in mathematical terms, fitness is the product of fertility and probability of survival. Evolution depends on this overall measure of reproductive success. Mating is one component of fitness, but a preoccupation with "mating success" has led to an emphasis on mating to the exclusion of other components of fitness. In reality, female choice considers the overall production of offspring, keeping mating in perspective. Darwin is incorrect in almost all details concerning female choice, although he must be credited with recognizing that female choice among animals exists in the first place.

What, then, are the preferences of female animals, and how do females vary in their preferences? What do females want from a male, how many times do females want to mate, how many males do females want to mate with, how does a female find Mr. Right, and how do females decide how many eggs to produce?

DEADBEATS NEED NOT APPLY

Is a male's true mettle tested in combat with other males? Does the best male surface as the winner and assume dominance over a hierarchy of wannabes? Shouldn't a female yearn to shack up with a proven winner? Shouldn't a female respect the winner of male-male competition as the best father for her baby, a stud with the best genes? Does mating with him guarantee the best and brightest child?

Let's see what female gobies think about male dominance. Sand gobies *(Pomatoschistus minutus)* are small fish (5 to 6 centimeters) common along European coasts. To see what a female goby wants in a male goby, specimens were collected from a shallow sandy bay near the Klubban Biological Station in Sweden and housed in seawater tanks for observation.[1] After the experiment, they were released back to the sea.

Sand gobies live for one or two years and experience one breeding season. Both males and females reproduce often during the breeding season, which is two months long (May and June). Males build nests under empty mussel shells by covering the shells with sand and excavating a cavity underneath. They attract females with a courtship display that includes showing their colorful fins. During spawning, a female attaches her eggs to the nest in a single layer.

In an experiment, two goby males were allowed to compete for a clay pottery fragment to use as a nest in order to determine the dominant male. The winner was usually slightly larger than the loser, although only by 3 millimeters. They were then placed in chambers at opposite ends of a tank. The tank was divided into thirds using transparent partitions. The middle chamber was left empty. The winner and loser were given new pottery fragments and allowed to build nests by themselves.

Next, a female was introduced into the middle chamber. The female could choose which of the males she preferred, indicated by the side of the chamber where she spent her time. After the female's preference was

determined, she was placed with one of the males, either the one she preferred or not, by flipping a coin, and then the time needed for spawning to occur was noted. Another female was placed with the remaining male, and the time they took to spawn was also noted. Thus both males were able to spawn.

Finally, after spawning, the females were removed, as were the partitions separating the males, leaving two males, each with a nest containing eggs, at opposite ends of the tank. A small crab was introduced, which is an egg predator. Observers counted the number of eggs lost to the predator in order to determine how good the males were at protecting the eggs.

The results are striking. Whether a male was dominant in competition for nests did not correlate with whether he was a good father in protecting the eggs. Also, female preference didn't correlate with dominance in male-male competition. The females didn't care if the male they preferred won his fight with another male. The females did care whether the male would protect the eggs. Somehow females were able to predict who would or wouldn't be a good father, and decidedly preferred mating with males who later turned out to be good egg protectors. A female could somehow look a male in the eye and tell if he was a deadbeat.

Now, let's take a look at the peacock wrasse *(Symphodus tinca)* that lives off the coast of Corsica in the Mediterranean in a shallow rocky habitat.[2] The female peacock wrasses have a choice of whether to lay eggs in a male's nest or to broadcast their eggs over the sea floor. Which they do depends on how they assess the offer of male parental care.

Large controller males construct guarded areas of a meter in diameter and place pieces of algae in the middle, to which the eggs attach. Nest construction takes one or two days, followed by two or three days during which females visit the nests and deposit about fifty eggs at a time, leading to as many as fifty thousand eggs in a nest. Thereafter, the male may guard the egg mass until hatching, which varies from twelve days in the cold water of mid April to six days in the warm water of mid June.

Smaller males take on two roles. They may be "followers," who swim at a distance behind gravid females and fertilize eggs broadcast on the open sea floor. Or they may hang out as end-runners around the territories of controllers and fertilize eggs laid in the territory. During the first half of the reproductive season, however, small males are absent. The

small males arrive only for the second half, presumably when the ability of the large male to shoo them away is constrained by the need to guard the eggs that have already been deposited.

Males defending eggs lose weight and appear to have a higher mortality during this period, so they abandon nests that haven't accumulated enough eggs to be worth their while. Abandoned eggs are hung out to dry, so to speak. Because abandoned eggs are concentrated in one spot, they quickly attract predators. Thus the best chance of an egg surviving is to be laid in a nest that is not abandoned, the next best chance is for an egg to be broadcast on the sea floor, and the worst is to be laid in a nest that is subsequently abandoned.

The males stay with only 20 percent of the nests early in the season, remain with 85 percent of the nests at midseason, and drop off to 20 percent again by the end of the season. Thus laying eggs in a male's nest is a good bet only in midseason. Indeed, only 15 percent of the females lay their eggs in nests at the beginning of the season, rising to 85 percent at midseason, and falling back to 15 percent as the season ends.

What does a female peacock wrasse want of a male? A male who isn't a deadbeat, who won't abandon her eggs. And she can tell. The investigators write, "If a female chooses to lay her eggs outside a nest, she tends to do so only after visiting several nests."

INVITING FEMALE COMMITMENT

How does a guy convince his gal that he isn't a deadbeat? Fish offer some advice on this ancient question too. Females know that males abandon nests that don't accumulate enough eggs to be worthwhile from the male standpoint. From a female's standpoint, adding eggs to an egg mass that's already large makes sense, because the male guarding it is more likely to stick around than if it was a small egg mass. So, how does an egg deposit get started? A female has to take a chance on a male or go it alone.

Various male fish have structures on their body that resemble eggs, a common example being the fantail darter *(Etheostoma flabellare)*. These small fish are found in freshwater streams in North America, including central Kentucky.[3] During the spring, males excavate nests beneath flat

rocks, defend small territories, and mate with various females who deposit eggs in their nests. Males then guard the eggs until hatching.

Each of the seven to eight dorsal spines on the male's front fin is tipped with a fleshy knob. These knobs are smaller than the size of real eggs but, on the largest males, approach the size of actual eggs. Deceit theorists have suggested that a female is fooled by these structures into believing that a male is already tending eggs, so that adding her own to the collection is safe. This hypothesized deceit is called "egg mimicry."

Two facts compromise this interpretation: females also have these fleshy knobs, and the knobs on males are smaller than real eggs. Why do females have these knobs if their only function is for males to deceive females? Why would these fish, who are visual predators, be fooled by fleshy knobs that are smaller than real eggs?

Experiments suggest that the females prefer to lay eggs in the nests of males with fleshy knobs rather than the nests of males whose knobs have been snipped off with scissors. Although the study was preliminary, we can still ask what such a result would mean. Were the females fooled? The alternative is that the fleshy knobs are symbols of eggs, not mimics of eggs. When a male swims close to the underside of a rock, he might be showing where the eggs should be placed.

Female fish want male fish to live up to their promise of guarding the eggs. The male must communicate that he is serious about his willingness to provide for the young. The invitation to lay eggs in his nest must somehow show he knows how to handle this responsibility. The female carefully assesses the credibility of the promise; she seems unlikely to be deceived by a trick such as egg mimicry.

HOW MUCH SEX IS ENOUGH?

Newspapers are filled with advertisements for new toys and chemicals to help people have sex more often. Well, how often is enough? Birds illustrate how females may take the lead in determining how often matings happen and when.

Female alpine accentors *(Prunella collaris)* from the central Pyrenees of France like sex.[4] These females don't worry about male harassment. If anything, it's the reverse—females harassing poor males into sex all the

time. What do these horny females want? They want the same thing female sand gobies and female peacock wrasses want: males who do their share of the housework.

Alpine accentors go in for eightsomes, as many as four males and four females. A female is fertile for about two weeks, from about a week before her first egg until the last egg is laid. After the eggs hatch, the males may help feed the young.

Fertile females actively solicit copulation. A female approaches a male, crouches with her breast touching the ground, lifts her tail to expose a bright red, swollen cloaca, quivers her tail from side to side, and shivers her wings. Just to be sure he's awake, she often jumps in front of him and presents her cloaca directly in his face. Hard to miss. A female solicits in this way once every 8.5 minutes. A full 93 percent of all solicitations are initiated by the female approaching the male, the other 7 percent by him approaching her.

The males in the group form a dominance hierarchy. The alpha male follows behind any fertile female, limiting but not entirely preventing lower-ranking males from approaching her. Moreover, the males play hard to get, ignoring 68 percent of the solicitations. Still, they do a lot of mating anyway. In fact, a female copulates 250 times per clutch of eggs, although a single insemination provides enough sperm to fertilize all the eggs. So much for believing that the sole purpose of copulation is to conceive!

What's going on here? An alpha male doesn't stick around to help at the nest unless he's sufficiently occupied at home. He can easily visit nearby nests, so to keep him at home, the female invests more time in mating with him than with the lower-ranking males. The lower-ranking males don't have as many opportunities to shop around outside the nest, but if they are to remain as helpers at the nest, they require some minimum share of the action. Therefore, a female actively displays to the subordinate males as well, making sure that they have some share of the copulations and therefore of the paternity.

Alpine accentors provide an example of females preferring the alpha male, because most of the copulations are with him and are initiated by the female. This preference might seem to suggest that the alpha male offers some benefit to the female, such as his "great genes," and that female preference for alpha males is an endorsement of their superior quality. The data show, however, that the quality of the chicks sired by an alpha male is no better than that of chicks sired by the subordinate males, judg-

ing by the weight of the chicks at the time they leave the nest. In fact, the only reason the female appears to prefer to copulate more with the alpha male is that the greater availability to him of opportunities outside the nest makes it more of a challenge to keep him at the nest. From the female perspective, copulation provides the shared paternity needed as a "staying incentive," which is allocated to males of various dominance status according to what is required to keep them involved at the nest.

Do monogamous females mate only during the brief period when the eggs are ready for fertilization? Or do monogamous females like fun too? In fact, monogamous females may be even more sexually active than females in other types of families.[5] In birds such as the mallard duck and common guillemot, mating starts before the female is ready to produce eggs, and before the male is ready to produce sperm. Why should all this mating occur when it is apparently not needed? The obvious answer, one might have thought, is that mating maintains the bond between male and female. Regular mating keeps the pair in touch with one another, so to speak. By mating, they enjoy sexual pleasure with one another. One might theorize that the pleasure of mating evolved in such species in order to provide an ongoing motivation for the members of the pair to stay together.

But in the minds of deceit theorists, "excess" mating between members of a pair has nothing to do with building relationships; rather, it represents females using sexuality to manipulate males into giving them free food—a dinner date followed by sex. According to one model for the evolution of "female sexuality" in monogamous birds, males keep buying dinner because they can't "risk leaving." As a result, "females benefit from the presence of males in such a way that males get nothing in return."[6]

For the record, biology provides no evidence whatsoever that the function of sexuality in monogamous relationships is deceit. Instead, theories of male/female cooperation should have been considered as a rationale for sexuality in the monogamous family.

WHEN FEMALES LOOK LIKE MALES

What does female-to-male cross-dressing tell us about the role of female choice? Reports on feminine males are marked by deceit rhetoric and

sensationalism. Reports of masculine females are scanty, suggesting underreporting. What emerges is that some females signal receptiveness with colors that coincidentally resemble male colors, whereas other females modify their attractiveness to males to control how often males solicit them.

At the northwestern tip of the Iberian peninsula lies the seaport city of A Coruña, Spain, where Bocage's wall lizard *(Podarcis bocagei)* lives. This lizard is the only vertebrate animal species so far in which females have been reported to imitate males, but the case isn't convincing.[7] Males have an intense green color on their back. Female wall lizards are usually brown, but when they have fertilized eggs already in their oviducts or have recently laid an egg, they turn green to signal that they won't accept courtship. Is being green masculine and therefore romantically unappealing to other males, as some scientists have speculated? Whereas feminine males are cast as deceivers, masculine females are cast as unattractive. Or could green simply be a gender-neutral signal telling males not to bother courting?

The green color seems to be a gender-neutral signal rather than a masculine presentation that males find unattractive, because males do occasionally try to mate with green females and are rebuffed. These males are presumably learning what green means. If males found green females unattractive, they wouldn't court them to begin with.

Interestingly, the phrase "male mimicry" is not introduced. Females are not seen as deceiving males. If this was a case of male mimicry, the males who do try to mate with green females would have to be mistaking the females as males and soliciting a same-sex courtship, something not (yet?) described in this species.

A comparable lizard species in western Ecuador, *Microlophus occipitalis,* also has females that display a special color when unreceptive to courtship.[8] Hatchlings of both sexes have red throats and chins for about a month. Then males lose the red pigment, while females retain some of the red in skin folds on the side of the neck. The males develop black markings on their back and grow larger than the females.

During the reproductive season, some females develop bright red pigmentation covering the throat and chin similar to that of juveniles. Imagine painting Texas-red on your chin and neck, all the way down to your breastbone: you'll get noticed. Females wear red on their chin and neck

when carrying undeveloped eggs in their oviducts or after laying eggs. Males were found to make more courtship approaches to nonred females and pursue the courtship with them more ardently. Conversely, red females rejected courtship advances more than nonred females did. Out of thirty-eight matings observed during three years of study, thirty-three involved either unpigmented females or ones with but a small trace of red, whereas only five involved fully red-throated females.

Thus females in both Spanish and Ecuadorian lizards signal when they are not receptive. In the Spanish species, the signal (green on the back) is a color that males coincidentally also have on their backs, whereas in the Ecuadorian species the signal (red on the chin and neck) is distinctive from the color that males have on their chins and necks. Bright colors have been described in the females of more than thirty species of lizards so far, and in eighteen of these, the bright colors are expressed when the females are carrying oviductal eggs.[9] Thus females using color to signal to males to back off is apparently quite general in lizards.

To find cases of genuinely masculine females, we visit the insects. Since the 1800s, naturalists have known that in many species, female damselflies appear in two color morphs, one distinctively female and the other resembling a male.[10] A species of damselfly from ponds in central Florida, *Ischnura ramburi,* has colorful males with green spots on the head, green on the thorax, and a black abdomen.[11] Feminine females have orange spots on their head, orange on the thorax, and a green-black metallic abdomen. (Gucci, are you listening?) The masculine females are green like the males but can still be identified by their female external genitalia and a bit of feminine color on the wings. What are we to make of these masculine females?

Male damselflies don't mate-guard. Instead, male and female damselflies take their sweet time in the mating itself. Copulation ranges from over one hour to over six hours, averaging three hours. While a long copulation might seem like great fun, this can waste a whole day and be too much of a good thing, especially if carried out day after day over a life span that is only a few days long.[12] Indeed, from a female's perspective, copulations beyond the first would be redundant, because one copulation supplies enough sperm. Extra copulations simply increase the risk of falling prey to some hazard.

The masculine females average half as many copulations as the feminine females. The behavior of a masculine female approached by a male resembles the behavior of a male to another male—a face-to-face standoff, like a baseball coach getting in the face of an umpire. Still, the masculine females definitely do mate, and therefore the males presumably do know what's happening.

A follow-up study on another species of damselflies, *Ischnura elegans,* shows that the advantage to a female of looking masculine depends on how many males are around. At high densities, masculine females benefited by avoiding sexual harassment from males and having freer access to water, where they could lay eggs with less disturbance compared with feminine females. But in sparse populations, masculine females were courted less by males and more often remained unmated compared with feminine females.[13] I find these damselfly cases convincing. Masculine females have a higher survival rate because of diminished harassment from males, but they can incur a lower chance of being mated.

Still, you never know what turns guys on. Although masculine females are in the minority (about 30 percent in most damselflies), in *Enallagma boreale Selys* the masculine females constitute about 60 to 80 percent of all females. In this species, males are actually attracted to the masculine females.[14] Thus what happens when a female looks masculine depends partly on male tastes.[15]

Some insect species have females that synthesize male perfumes, reversing what we saw in garter snakes. Females use these perfumes to keep males away—like a woman wearing after-shave lotion. To unload a guy, wear Jade East on your next date! During mating, a male fruitfly *(Drosophila melanogaster)* transfers an "antiaphrodisiac" to the female. Although most evaporates four to six hours after the first mating, females later synthesize this compound themselves during courtships, making them less attractive to males.[16] Butterflies also use antiaphrodisiacs.[17]

Well, at this point you might conclude that vertebrates offer no examples of masculine females because the colors in female lizards that signal an unwillingness to mate are only occasionally the same as male colors, hence the overlap is probably coincidental. True, the most extensive studies of masculine females come from insects. But recall the Andean hummingbirds and the hooded warbler of the eastern United States, both cited in chapter 6 as examples of species with transgender expression. In

fact, female hummingbirds and female hooded warblers introduce the phenomenon of "female ornaments." Here's where the underreporting of gender variation in females is taking place.

Female ornaments in birds are brightly colored feathers, skin flaps, beaks, and crests that are found in males and also expressed in a few females. Darwin suggested that female ornaments were male traits being "accidentally" expressed in females because the genetic system in females wasn't up to the task of shutting off their development during embryogenesis. Today, interest increasingly focuses on how females benefit from these traits. Other birds with ornaments causing some females to resemble males include the crested auklet, feral pigeon, barn swallow, bluethroat, blue tit, house finch, and zebra finch.[18]

Among wattled starlings *(Creatophora cinerea)*, grassland birds of eastern and southern Africa, most males develop a special appearance during breeding season consisting of two hanging skin flaps (wattles) on each side of the beak, loss of feathers from the head to expose yellow or black skin underneath, and fleshy combs on the forehead. (The feather loss has been compared to male pattern baldness in humans because both are brought about by male hormones.) About 5 percent of the females also develop these fleshy folds and feather loss, qualifying them as masculine females. Not much else is known.[19]

Female deer with antlers, usually a trait limited to males, might be thought of as masculine females. In white-tailed deer *(Odocoileus virginianus)*, 1 percent of the females have antlers, and antlers are reported in some female black-tailed deer *(Odocoeleus hemionus)* as well.[20] In reindeer *(Rangifer tarandus)*, females usually have antlers, as do the males, but not every female—the frequency is anywhere from 8 to 95 percent, depending on the population.[21] Thus many deer species offer the possibility of looking further into why females might adopt a masculine appearance.

FINDING MR. RIGHT

Sometimes it's hard to get enough information about prospective mates. Some male genders appear to help bring couples together, like the medium-sized male sunfish (see chapter 6). Here's a similar case involving birds who mate in leks, just like sunfish do. A lek is a male red-light district in which males congregate, each defending a personal space within this patch, called his "court." Females come to the lek, and each male tries to attract a female onto his court so they can mate there. From a female's point of view, what basis is there for choice? How to find Mr. Right?

Ruffs *(Philomachus pugnax)* are sandpipers—shorebirds that breed during the summers in northern Europe from England to Siberia.[22] Ruffs owe their name to a ring of feathers around the neck of the male that is reminiscent of the large collars, or ruffs, worn in the Renaissance. Male ruffs occur in at least two genders. One gender has a dark ruff, accessorized with dark feathers on the head to make a tuft, while the other has white feathers in both ruff and tuft. These genders are genetic, with about 20 percent white-ruffed, and the remaining 80 percent black-ruffed.

Ruffs mate in leks, but not exclusively so. Males also follow females as they forage, displaying to them while they are feeding. If the resources are so spread out that the female density is thin, males stop following females and instead congregate in a lek, letting the females come to them.[23] At a site in Finland, 12 percent of the males participated in a lek, and 90 percent of the displays to females took place outside of leks.[24] Males off the lek spend 75 percent of their time feeding and the rest trying to attract a female. On a lek, males have a mating rate five times higher than in the fields, despite all the effort spent displaying to females while off lek. A female off lek is busy feeding too, and her mind is on other matters. Females who go to a lek have the same thing on their mind that males do—sex, sex, sex.

What differentiates the ruff from other lekking birds is its two male genders. The dark-ruffed males are controllers who defend small courts of about 1.5 square meters against other dark-ruffed males on the lek. White-ruffed males are solicited to join as assistants. When a white-ruffed male is nearby and a dark-ruffed male is alone on a court, the dark-ruffed male does a half-knee bend and bows his bill downward. This invites the white-ruffed male to join him on the court.[25] Females who arrive at the lek prefer a dark/white team rather than a single dark-ruffed male. Both males jointly court and then mate with the female. While mating, a dark-ruffed male may try to limit the white-ruffed male's

access to the female, short of actually evicting him. A dark-ruffed male obtains more matings when a white-ruffed male is present than when alone, even though the matings are shared. Thus the two male genders act as controller and cooperator. Somehow the cooperator assists the controller in providing a more attractive mating court, and in return is paid a staying incentive of shared matings. The two genders exist specifically to address the demands of female choice.

I haven't located any theories about why a female finds a court with a dark/white team more attractive than a court with a single dark-ruffed male. Most investigators seem to assume that a female automatically finds two males better than one—the more masculinity the better. If more total masculinity is so important, then two dark-ruffed males could simply team up with each other. Why two genders? My hunch is that a white-ruffed male builds relationships with the females while he is with them off the lek. While the dark-ruffed male is defending a court from other dark-ruffed males, the white-ruffed male is flying with females in the field and presumably getting to know them. Perhaps the white-ruffed male can, so to speak, make introductions when the females arrive at the lek. He can facilitate a mating by knowing the females after having spent time with them, and also by knowing the dark-ruffed male after their initial courtship together. He can act as a go-between, a marriage broker.

FAMILY SIZE

Who determines the size of a family? From an evolutionary standpoint, family size is ultimately controlled by a female determining the size and number of eggs she lays. A female chooses an egg size and number based on the parental investment she expects to provide plus a discounted expectation of what the male will contribute to their combined investment pool. In mammals, a female may also be coerced by a controlling male to produce more young than she would if allowed reproductive freedom. Little is known about female choice of family size among vertebrates. More attention has been focused on female choice of mates and frequency of mating.

Females of the side-blotched lizard *(Uta)* have two color morphs, yellow and orange, which differ in egg size and egg number, as mentioned in chapter 6. In salmon, the largest egg can be two to three times the size of the smallest egg. Since they start with the same amount of material to put into eggs, this egg-size variation translates into some families being up to three times bigger than other families.[26] A large variation in egg size has also been noted in some bird species.[27]

Family size is one aspect of reproductive choice. Do females control their reproductive destiny? In biology, the traditional assumption has been that a female sets the number and size of the eggs she produces, and the males fight it out among themselves to acquire paternity of those eggs. An alternative theory is that female choice of mating partners allows a male to cooperate with her in jointly setting the family size. If a male promises to assist with parental care and doesn't defect, the female can elect to have more offspring than she would have if she were raising them alone. This cooperative solution to family size would generally lead to higher egg production than a competitive solution would. The role of courtship may be more to establish mutual trust that a cooperative solution will be honored than for the male to advertise his qualities, power, and possessions.

NUMBER AND IDENTITY OF PARTNERS

Another aspect of female reproductive choice is the number and identity of mating partners. Female partner choice is yet one more area of biology showing severely biased language. Studies describe females who prefer one mate as "faithful" and females who prefer multiple mates as "promiscuous." A clutch of eggs with multiple paternity is said to contain "legitimate" and "illegitimate" offspring, and a male tending a clutch with multiple paternity is said to be "cuckolded." This overlay of moralizing obscures the facts.

Razorbills *(Alca torda)*, colonial seabirds of the North Atlantic, have been studied on Skomer Island off the coast of Wales.[28] Males and females have the same color and overall shape and live in pairs at nests in a colony. A pair provides joint parental care for one egg laid each year, which can be thought of as economic monogamy. Yet, as we saw in

chapter 5, an economically monogamous pair is not necessarily reproductively monogamous.

Openly visible areas, called arenas, are located near the colony. Most mating occurs in the arenas, even that between bonded pairs. Approximately 75 percent of the within-pair matings take place in the arena, even though the pair shares a nest in the colony, while 87 percent of the extra-pair matings occur in the arenas. A goodly number of same-sex matings occur there too (see p. 136).

One-third of the females accepted extra-pair matings, while two-thirds did not. Over two consecutive years, the identities of the females who did, or did not, accept extra-pair matings remained the same. Of the females who did accept extra-pair matings, most accepted only one, and the remaining accepted matings with two, three, or even seven other males. The investigator concluded that two types of females exist: two-thirds "faithful" and one-third "promiscuous."

All the males participated in extra-pair mating attempts. The males who pair-bonded with promiscuous females were slightly more successful in obtaining extra-pair copulations (EPCs) themselves than males paired with faithful females. The investigator concluded that all guys normally play around, although playboys tend to pair-bond with playgirls.

Why was this study done? To decipher the feminine mystique. The investigator writes, "The benefit of EPC's to males is clear; by fertilizing additional females, males can increase their reproductive success at the expense of other males. . . . While it is now clear that some female birds pursue EPC's, the possible benefits accruing to females remain obscure." The list of conjectured reasons for why a female might want to mate with more than one male includes wanting great genes, wanting a variety of genes, storing sperm in case one of the males turns out to be infertile, and checking him out in view of switching later. These conjectures assume that all a guy delivers is genes.

Let's think. Could mating involve more than the transfer of sperm? Indeed, why is the mating being done in open arenas? Even the within-pair matings? So everyone can see, of course! Public matings have symbolic significance. If a birdwatcher can see the matings, so can the birds. Not only is the mating done in public—the mating act is often just for show. Female razorbills can control whether sperm is transferred. Females have

long, stiff tails that they must lift for the male to make cloacal contact. Females can carry out copulatory behavior, including being mounted, while preventing sperm transfer. In over six hundred extra-pair copulations, observers never saw a male force a female to lift her tail and make cloacal contact. The investigators conclude that males "do not appear capable" of forcing a copulation. But perhaps males don't want to force a copulation. Perhaps the show of copulation is what's important, not the sperm transfer.

The focus on sperm transfer as the sole purpose of copulation leads to one difficulty after another. If a male is truly "cuckolded," he should abandon his unfaithful mate. Male razorbills do not abandon their mates, nor do they attack them when they accept an EPC. Nor do male razorbills reduce their parental care in proportion to their mate's promiscuity. Why not? Didn't they read the book? Are females getting away with something that males must grudgingly tolerate?

The story doesn't add up. I suggest instead that mating is as much about managing relationships as about the transfer of sperm. By mating in public arenas, both males and females are advertising the network of relationships they participate in. Two-thirds of the females apparently find it advantageous to concentrate the paternity of their eggs in one male, and one-third to distribute the probability of paternity across several males. Because this arrangement has been broadcast to the entire colony by mating in public, the alliances and power relationships that flow along this network of relationships are publicly known too.

But why might some females want to distribute the probability of paternity and others not? What are the implications of a network of power relationships for birds? Because the males do not prevent females from distributing the probability of paternity or retaliate against them, could they too be benefiting from the formation of a network of alliances?

Consider another colonial species. Like razorbills, female tree swallows *(Tachycineta bicolor)* from Ontario, Canada, are reported to have "two alternative copulation strategies."[29] These birds were also studied to decipher the feminine mystique. The investigators write, "Previously, much attention was focussed on benefits to males. . . . Later, it was realized . . . that females may not be just passive targets for EPC." Hello! The investigators continue, "The conflict between the extra-pair male and the pair male is obvious and straightforward; the extra-pair male

will seek to enhance his reproductive success at a relatively low cost by parasitizing the parental care of the pair male, whereas the pair male will try to protect his paternity and avoid caring for unrelated offspring. The interest of the female seems more obscure." Again, the investigators admit they don't understand the females. They also disparage the EPCs as a theft of the parental care that rightfully belongs to the pair male, never considering that the pair male might be trading some of the probability of paternity that he apparently controls in return for some benefit. The investigators conclude, "In some species, females actively seek EPCs . . . in other species females are generally resistant toward copulation attempts by non-mates."

To find out why females stray from their marriage vows, the investigators first tried to determine if only certain females do. Surveys of paternity using DNA fingerprinting showed that 50 percent of nests contained one or more nestlings sired by an extra-pair male. Furthermore, a brood with extra-pair paternity (EPP) didn't contain just one "illegitimate" nestling; 65 percent of the nestlings were sired by extra-pair males. So half of the females lay clutches with no extra-pair eggs, and the other half of the females lay clutches with a majority of eggs fertilized by extra-pair matings.

In an experiment, ten females were allowed to lay an egg or two and then the pair male was removed (shot). The "widow" was then allowed to acquire a replacement male. The first two eggs would have been fathered by the original pair male if the female was a stay-at-homer, but by diverse males if she was a swinger. Would the replacement male father the remaining eggs? The stay-at-homer females declined to copulate with the replacement male and used stored sperm from the original pair male to fertilize subsequent eggs, so that 78 percent of the eggs laid after the first two were still fathered by the original pair male, even though he was now dead. The swinger females, however, readily copulated with the replacement male. But the eggs laid after the first two often were fertilized not by the replacement male but by other, neighboring males. The swinger stayed a swinger, and her brood continued to be fathered by multiple males, while the stay-at-homer remained "faithful" to her original pair male.

The investigators invite the possibility that "the two types of copulation behavior are obligate strategies, i.e., that some females are always faithful while others are always promiscuous." One-third of the extra-pair matings were solicited by a female who flew to the nest of another male and mated with him there, while the remaining two-thirds took place at the nest of the female, with a male who came to her. "The ability of females to effectively resist copulations may also explain why forced EPC attempts are rarely seen." Thus the responsibility for playing around rests with the females who volunteer to play.

How do the males react to "their" females playing around? The investigators say that mate guarding is not possible in colonial species because males must guard nests and can't guard the females themselves. Instead, males copulate frequently. Fifty copulations occur per clutch, when one is enough. Thus, according to this theory, females play around because the homebound males can't guard them. Instead, males mate extensively when the females return home after a night on the town, hoping their sperm will outnumber the sperm from any other males the female played around with. Still, the males don't copulate any differently when their mate is a swinger versus a stay-at-homer. For this reason, the theory claims that "the males cannot be sure whether or not their mates are faithful."

Keep in mind that the copulations take place in the open, where birds as well as birdwatchers can see them. I can't imagine any reason why the males are always unaware of the copulation history of their pair mate. Furthermore, recent copulation doesn't guarantee paternity, because females can fertilize eggs with stored sperm. Finally, a goodly number of the EPCs are actually same-sex matings between males (see p. 137).

Again we have a story that doesn't add up. The theory doesn't offer any reason why some females accept extra-pair matings and others don't. The theory doesn't explain why males should care more about defending the nest instead of guarding the female, nor why males should be seemingly indifferent to whether their pair mate is a stay-at-homer or a swinger. The overlooked clue is that replacement males are unhelpful, even dangerous. In an undisturbed nest, males make half of the trips to bring food to the nestlings, so male and female share this workload equally. In nests where the original male was removed after only one egg was laid, the replacement male defended the nest real estate, but only half of these males provided any food to the nestlings, and the remainder completely ignored the nestlings' need for food. In these cases, many

nestlings died from starvation because the female couldn't fully compensate for the lack of male cooperation.

Even more dramatically, if the original male was removed after two or more eggs were laid, the replacement male actually killed the nestlings. Thus a male who takes over an undefended nest when it already contains a few eggs is certain to commit infanticide. The observation of male infanticide is not new. In a pioneering study twenty-five years ago, Sarah Hrdy showed that female langurs (an Indian monkey) distribute paternity to purchase protection against male infanticide.[30] I suggest that some female tree swallows also deliberately distribute the probability of paternity among the males most likely to take over the nest if the original male is lost. A female can allocate all the probability of paternity to the nest male if she feels he is not likely to die or be evicted and wants maximum parental assistance from him.[31] Or she can distribute the probability of paternity among the males likely to take over the nest if the risk of losing the nest male seems high, thereby ensuring some safety for her offspring.

Now, the nest male may even agree to "his" female distributing the probability of paternity to neighboring males. If his neighbors have some likelihood of paternity in his nest, there is less chance that they will wish to evict him, or kill his brood if he dies. Regardless of how often biologists claim that the only goal of a male is to fertilize as many eggs as possible, in fact the male also has an interest in whether the eggs successfully hatch. A male's parental care need not be limited to providing food for the nestlings, but can extend to ceding some probability of paternity in order to help ensure the survival of the nestlings he is helping to feed. The female's distribution of paternity among males may amount to a "peace incentive" to purchase protection for her brood, a household expense that the male approves of. Of course, the male may work to keep this expense as low as possible by mating extensively with the female when she comes home for the night, but monitoring a cash flow is different from trying to close an account.

We need not think of tree swallow females either as choir girls honoring their marriage vows or as loose women cheating on their husbands. Instead, females may be part of a social system for raising young, in which they allocate matings so as to balance the danger of male power with the benefit of male parental investment, all with the acquiescence of the

males. The social system thereby decouples economic monogamy— male and female working together to feed the young at a nest— from reproductive monogamy (compare discussion in chapter 5 of decoupling in the closely related cliff swallows).

More generally, I'm suggesting that females publicly choose mating partners to manage the genetic relationships of their offspring. Females guarantee their offspring safety by buying membership in the old genes club and choose their extra-pair partners with the tacit consent of the pair male. Females choose not males with supposedly "great genes," but males with well-connected genes. In genetic lingo, females are concerned with genetic identity by descent, not genetic identity by state. When a female chooses a male with some special color on his tail, she is not following the dictates of some inexplicable taste for fashion, but rather endowing her offspring with a bodily marker of culturally inherited power, like the Tudor nose.

Thus Darwin was fundamentally on the wrong track in his conceptualization of female choice. Sand guppies and alpine accentors show that dominant males don't have any better genes than subordinate males, according to any known metric (such as the weight and vitality of the nestlings). Sand guppies and peacock wrasses demonstrate that females choose males not for their great genes but for the likelihood of actually delivering on their promise of parental care: females are looking to avoid deadbeats. Alpine accentors and tree swallows suggest that females may choose males to distribute the probability of paternity so as to balance the incentive for a male to provide parental care with the danger to her nest from other males.

Damselflies reveal that females may tune their gendered presentation to control the number of male advances. Female wattled starlings, hooded warblers, reindeer, and other females with male ornaments suggest that gendered symbolism may also be tuned among vertebrates to regulate the frequency of male advances.

The side-blotched lizard shows that females can vary family size by varying egg size, inviting the suggestion that family size is set to accommodate the discounted expectation of male parental care. Courtship is then not about a male advertising great genes to a female, but rather a negotiation over the degree of parental care the male will provide, together with the female's assessment of the credibility of the male's prom-

ise. To aid in this assessment, a female may require the services of a marriage broker to testify on behalf of a male. The cooperator morphs in bluegill sunfish and ruffs are apparently male genders that evolved to fill this need for a go-between, suggesting that female choice has contributed to the evolution of gender multiplicity among males.

This sophisticated constellation of decisions that females make about males goes far beyond the simplistic conceptualization that Darwin put forth that all a female is searching for is a hulk with great genes.