

# 16 • Communication and the evolution of alternative reproductive tactics

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## CHAPTER SUMMARY

In this chapter, concepts derived from communication network theory are applied to the understanding of the evolution of signals in species with alternative reproductive tactics (ARTs). These species are particularly interesting to consider from the perspective of communicating in a network because the signaling and receiving behavior of different reproductive phenotypes can be expected to be subject to diverse selection pressures. We begin by briefly introducing ARTs and communication networks. Then the consequences of communicating in a network are considered from the perspective of the several reproductive phenotypes occurring in species with ARTs, both as signalers and receivers. Finally, the evolutionary outcome of conflict and cooperation between these reproductive phenotypes is predicted in an integrative approach, and new directions are proposed to test some of the hypotheses derived.

## 16.1 INTRODUCTION

Alternative reproductive tactics (ARTs) is the term used to refer to variation in mating behavior found within a species. As the topic is the subject of this book, we will only briefly introduce ARTs in relation to signaling. More detailed information on ARTs can be found in several chapters in this book and recent reviews (e.g., Brockmann 2001, Shuster and Wade 2003).

For simplicity, we have only considered male ARTs. This choice reflects the facts that male ARTs are more common than female ARTs (but see Alonzo, Chapter 18, this volume) and that many more examples of male ARTs have been described. Nevertheless, the ideas presented here extend directly to female ARTs. The bias towards fish examples in this chapter reflects the abundant literature on fish ARTs.

### 16.1.1 Bourgeois, sneaker, female-mimicking, and cooperative males

Males may reproduce by investing primarily in direct access to, and defense of, reproductive resources (“bourgeois males”). Other males may access these resources either by a quick and inconspicuous approach (“sneaker males”), by mimicking females (“female mimics”) or by cooperating with bourgeois males (“cooperative males”) (Taborsky 1994, 1997, 1998, 1999).

Sneakers and female mimics are expected to decrease the bourgeois male’s success. For example, in the beetle *Onthophagus taurus*, the bourgeois male’s share of paternity declines with increasing sneaking pressure (Hunt and Simmons 2002). Contrarily, cooperative males are subordinates who overall increase the bourgeois male’s reproductive success by investing in female attraction, territory defense, or parental care. As an example, in the cooperatively breeding fish *Neolamprologus pulcher*, subordinate males increase the reproductive success of the bourgeois male by helping with parental duties and territory defense (Brouwer *et al.* 2005) and these cooperative males benefit by siring some of the offspring (Balshine-Earn *et al.* 1998, Dierkes *et al.* 1999). Sharing of reproductive resources is usually explained by two types of models: optimal skew models assume that bourgeois males control the access to reproductive resources and allow cooperative males to access resources in exchange for their cooperative efforts, and incomplete control models assume that cooperative males forcibly gain access to those resources due to incomplete control by the bourgeois male, thus also reproducing parasitically (e.g., Emlen *et al.* 1998, Reeve *et al.* 1998, Johnstone and Cant 1999, Kokko 2003). In both cases, however, conflict between bourgeois and cooperative males occurs on the level of access (allowed or forced) to reproductive resources.

## 16.2 COMMUNICATION NETWORKS

Signals produced by animals are often detected by more than one receiver simultaneously. As a result, most animals communicate in a network with several individuals occurring within communication distance (McGregor 1993, McGregor and Dabelsteen 1996). However, although conflict and cooperation between senders and receivers have long been recognized as selection pressures shaping the nature and design of signaling and receiving systems (e.g., Dawkins and Krebs 1978, Krebs and Dawkins 1984), only recently has the role of other parties in a communication network (e.g., eavesdroppers or audiences; see below) been considered when studying the evolution of communication (e.g., Johnstone 2000, 2001).

### 16.2.1 Eavesdropping

A consequence of animals communicating within a network is that information produced by a signaler is more widely available than the signaler–receiver dyad that is usually considered. An important class of such extra receivers has been termed “eavesdroppers” (McGregor 1993, McGregor and Dabelsteen 1996). Recently, Peake (2005) has clarified the definition of eavesdropping in the context of animal communication as “the use of information in signals by individuals other than the primary target.” We will use this

definition throughout. One reason for doing so is that it specifically avoids the effects of the presence of eavesdroppers on communication, and this is important because eavesdroppers can confer benefits as well as impose more obvious costs. Peake (2005) has also made a distinction between two types of eavesdropping. *Interceptive eavesdropping* refers to the use of information contained in a signal intended (in the evolutionary sense) for another individual, as, for example, when a bat locates a male frog based on the calls produced to attract female frogs (Figure 16.1A). Interceptive eavesdroppers usually use broadcast signals as the source of information, are usually heterospecifics, and generally produce a negative or zero pay-off to signalers (Peake 2005). *Social eavesdropping* refers to the gathering of information from signaling interactions between conspecifics in which the eavesdropper plays no part. For example, in the fighting fish *Betta splendens*, males pay more attention to a pair of interacting than noninteracting males and are more reluctant to approach and display towards a male that they have observed winning an interaction than towards a loser, but there is no such difference in response to males that have won and lost interactions out of sight of the subject (Oliveira *et al.* 1998) (Figure 16.1B). Social eavesdroppers thus extract and may use detailed information from social interactions, and this may result in a negative, neutral, or positive pay-off to signalers (Peake 2005).

(A) Interceptive eavesdropping



Figure 16.1 Two distinct types of eavesdropping. (A) In interceptive eavesdropping information contained in a signal intended for another animal is used. In the example, frog-eating bats locate prey by intercepting their mating calls. (B) In social

(B) Social eavesdropping



eavesdropping animals use information gathered during signaling interactions. For example, eavesdropping males of the fighting fish *Betta splendens* are less likely to initiate a fight with a male observed winning an interaction than with a loser male. (After Peake 2005.)

### 16.2.2 Audience effects

During a social interaction, signalers may also adjust their behavior according to the presence and nature of animals other than those directly involved in the interaction. This has been termed the “audience effect,” and it has been demonstrated in a number of species (e.g., Evans and Marler 1984, Gyger *et al.* 1986, Hector *et al.* 1989, Marler and Evans 1996, Doutrelant *et al.* 2001, Matos and McGregor 2002, Matos *et al.* 2003, Dzieweczynski *et al.* 2005; reviewed by McGregor and Peake 2000, Matos and Schlupp 2005). For example, male fighting fish change the nature of their aggressive displays during male–male agonistic interactions depending on the gender of the audience (Doutrelant *et al.* 2001, Matos and McGregor 2002, Dzieweczynski *et al.* 2005). In nature, audiences are also likely to act as eavesdroppers on most occasions. For example, during a male–female sexual interaction, the presence of another female may create an audience effect (i.e., influence the displays of the sexual pair), and at the same time, she may be a social eavesdropper (i.e., collect and use information from the interaction between the pair). For simplicity, we will assume that all audiences are possible eavesdroppers and are considered as such by signalers (for a discussion of the distinction between apparent and evolutionary audiences, see Matos and Schlupp 2005).

### 16.2.3 Fitness consequences of eavesdropping

The effect of eavesdropping on the general design of signaling and receiving systems will depend on its fitness consequences to both signalers and receivers. It is probably reasonable to assume that if an animal eavesdrops it has, on average, benefited from the behavior in the past. It is less straightforward to make generalizations about the animals that are eavesdropped upon, particularly those involved in a signaling interaction where several combinations of fitness consequences are possible, including different consequences for each individual. The examples below illustrate the range of outcomes expected from the occurrence of eavesdropping.

#### EAVESDROPPERS HAVE FITNESS COSTS

If eavesdropping is common and has a fitness cost for both signalers and receivers, eavesdropping pressure should promote inconspicuous, cheap, and directional signals (i.e., “conspiratorial whispers”: Dawkins and Krebs 1978, Maynard Smith 1991, Johnstone and Grafen 1992, Johnstone 2000). Examples of animals decreasing signal

intensity with increasing eavesdropping pressure are common: several species of petrels stop producing mating calls when playback simulates the presence of a predator (Mougeot and Bretagnolle 2000), and pipefish *Syngnathus typhle* decrease courtship display frequency and take longer to court females with increasing eavesdropping pressure from predators (Fuller and Berglund 1996).

#### EAVESDROPPERS HAVE FITNESS BENEFITS

If eavesdropping benefits the signaler and is positive or neutral for receivers, signals should contain features that enhance information transfer to eavesdroppers. For example, during sexual interactions females may copy the mate choice of other females and prefer to associate with males previously observed in the company of females (e.g., Dugatkin and Godin 1992). A successfully courting male is likely to gain fitness benefits (e.g., more matings) if other females eavesdrop upon its interaction with the primary female. The primary female may not suffer any cost from eavesdropping females; indeed, it may even gain benefits as in species where the probability of nest abandonment by males decreases with increasing numbers of eggs or young in the nest (e.g., Taborsky *et al.* 1987). There is abundant empirical evidence that successful males use more conspicuous displays during sexual interactions than less successful males, but whether this aims, at least partially, to enhance information transfer to eavesdropping females is unclear.

#### EAVESDROPPERS HAVE BOTH FITNESS COSTS AND BENEFITS

Eavesdropping may have opposite fitness outcomes on interacting individuals. For instance, a proposed function of long-range copulation calls by females in birds and mammals is to attract not only the pair male but also extra-pair males in order to promote male–male competition and possibly gain both direct and genetic benefits (e.g., Cox and La Boeuf 1977, Birkhead and Møller 1992). The paired male may pay a cost if eavesdropping occurs (e.g., lost fertilizations), and females may gain from eavesdropping (e.g., the eavesdropping male may be of superior quality). In these cases signals will result from a compromise between costs and benefits for signalers and receivers. In this example, paired males may be unresponsive to female signals above a certain threshold or may punish females observed signaling to extra-pair males (e.g., Valera *et al.* 2003). Females should signal at a level where benefits of extra-pair male attraction compensate the costs of retaliation by the paired male.

### 16.3 COMMUNICATION AND ARTs

The adaptive significance of morph-specific traits that are such distinctive features of ARTs has been thoroughly investigated, but little attention has been devoted to the role of conflict and cooperation between signalers, receivers, and eavesdroppers in shaping the evolution of communication traits in the context of ARTs. In other words, some of the differences observed between alternative reproductive morphs may relate to their different roles in the communication network environment. For example, sneakers or female mimics have opposite fitness consequences for bourgeois males. Therefore, we might expect cooperative males to signal their tactic to bourgeois males while sneakers and female mimics should not. Such differences will result in different selection pressures acting on the signaling and receiving systems of the various alternative reproductive phenotypes, leading to differences in their sensory and receiving systems. In this section, we explore in detail the influence of intraspecific interactions on the signaling and receiving behavior of bourgeois males, females, and parasitic or cooperative males.

#### 16.3.1 The bourgeois male perspective

##### SIGNALING BEHAVIOR IN RELATION TO EAVESDROPPING PRESSURE

Bourgeois male sexual signals should attract females while minimizing the likelihood of sexual parasitism by other males. These are conflicting interests as signals produced by bourgeois males for female attraction may be subject to eavesdropping by other males seeking access to the bourgeois males' reproductive resources. Thus, in species with ARTs, bourgeois male sexual signals generally represent a trade-off between female attraction and attracting unwanted male competitors (Table 16.1, Figure 16.2). If eavesdropping by other males decreases the bourgeois male's reproductive success, this should promote a decrease in the conspicuousness of sexual signals produced by the bourgeois male (e.g., intensity, frequency) as eavesdropping pressure increases.

Many examples have been described in support of this prediction, probably because in several species both bourgeois males and females do not benefit from advertising mating events to eavesdropping males. One such example is the Mediterranean wrasse *Symphodus ocellatus*. In this species bourgeois males actively defend a nest and court females while smaller sneaker males stay close to actively spawning nests and try to achieve parasitic fertilizations of

eggs (Taborsky *et al.* 1987, Taborsky 1994). The reproductive success of both bourgeois males and females decreases with increasing parasitic pressure (Alonzo and Warner 1999, 2000). Field experiments have shown that bourgeois males dynamically adjust their signaling behavior according to parasitic pressure. As predicted, when the number of sneakers in the vicinity of nests was experimentally decreased, a larger number of bourgeois males courted females (Figure 16.3A), and the reverse was true when there was an increase in the number of sneakers (Figure 16.3B) (Alonzo and Warner 1999, 2000; see also van den Berghe *et al.* 1989). The male's unresponsiveness to females leads to a decrease in the number of sneakers in the vicinity of the nest that potentially increases the bourgeois male's future reproductive success by decreasing parasitic fertilizations of eggs (Alonzo and Warner 1999, 2000). Similar results were found for the three-spined stickleback *Gasterosteus aculeatus*, where bourgeois males reduce their courtship rate towards females in the presence of potential sneakers (Le Comber *et al.* 2003).

Besides decreasing the conspicuousness, frequency, or duration of signals in the presence of eavesdroppers, bourgeois males may also include signaling components that diminish the probability of eavesdropping. This has been suggested for an Australian bushcricket of the genus *Caecidia*. In this species calling males add a loud chirping sound, not used in female attraction, to the end of their female-calling song. Females respond with a short click soon after the male call. Hammond and Bailey (2003) suggest that the chirping component of the male call masks the female response so that eavesdropping males are unable to intercept the female based on her response. The authors also suggest that the calling male is likely to be able to hear the female response shortly before or during pauses in the syllables of the mask while an eavesdropping male will not.

However, bourgeois males will have higher reproductive success if cooperative males are attracted by their signals (this is still eavesdropping by Peake's [2005] definition, because the primary targets are females). In this scenario, bourgeois male sexual signals should become more conspicuous when the benefits of attracting other males (e.g., an increase in female attraction) outweigh its costs (e.g., lost fertilizations: Figure 16.2C). The hypothesis that male sexual signals directed to females may incorporate conspicuous features to promote interception by eavesdropping cooperative males has not been investigated. Bourgeois males may also signal directly to other males in order to promote their cooperation. For example, in the lek-breeding ruff,

Table 16.1. A hypothetical example of variation in female and parasitic male attraction in relation to the intensity of a sexual signal produced by a bourgeois male

| Signal intensity | Number of females attracted | Total number of eggs laid <sup>a</sup> | Number of parasitic males attracted | Total number of eggs fertilized by parasitic males <sup>b</sup> | Proportion of eggs fertilized by the bourgeois male | Total number of eggs fertilized by the bourgeois male |
|------------------|-----------------------------|--|-------------------------------------|---|---|---|
| $I$              | $F$                         | $E = F \times 10$                      | $P$                                 | $L = (P \times E) / 10$   | $M = (E - L) / E$                                   | $S = E - L$   |
| 1                | 1                           | 10                                     | 1                                   | 1   | 0.9   | 9   |
| 2                | 2                           | 20                                     | 2                                   | 4   | 0.8   | 16  |
| 3                | 3                           | 30                                     | 3                                   | 9   | 0.7   | 21  |
| 4                | 4                           | 40                                     | 4                                   | 16  | 0.6   | 24  |
| 5                | 5                           | 50                                     | 5                                   | 25  | 0.5   | 25  |
| 6                | 6                           | 60                                     | 6                                   | 36  | 0.4   | 24  |
| 7                | 7                           | 70                                     | 7                                   | 49  | 0.3   | 21  |
| 8                | 8                           | 80                                     | 8                                   | 64  | 0.2   | 16  |
| 9                | 9                           | 90                                     | 9                                   | 81  | 0.1   | 9   |

<sup>a</sup> Assuming each female lays 10 eggs.

<sup>b</sup> Assuming each parasitic male fertilizes 10% of the eggs.

#### Box 16.1 Lek breeding: the ruff

In the lek-breeding ruff, *Philomachus pugnax*, “independent” males defend territories inside leks where many males aggregate to perform sexual displays towards females. Nonterritorial “satellite” males move between territories, displaying in the independents’ courts and trying to copulate with females when they enter the territory (Hogan-Warburg 1966, van Rhijn 1991, Höglund and Alatalo 1995, Lank *et al.* 1995, Hugie and Lank 1997). Independent and satellite alternative strategies are genetically determined, and independents have darker plumage than satellites (Lank *et al.* 1995). Breeding plumage is highly variable between individuals but highly stable within the same animal (Lank *et al.* 1995), and territorial males can presumably individually identify satellite males by their plumage (Lank and Dale 2001). Larger leks are preferred by females that seem to be attracted to territories with both types of males (van Rhijn 1973, Lank and Smith 1992, Höglund and Alatalo 1995, Höglund *et al.*

1993, Widemo and Owens 1995, Widemo 1998). Independents try to recruit satellites into their territory by directing signals to satellites similar to those produced during courtship sequences (Figure 16.4A). Independent male’s reproductive success is predicted to be maximum in intermediate-sized leks, as a decrease in the proportion of copulations attained by the territorial male in larger leks offsets the increase in female visits (Widemo and Owens 1995, 1999) (Figure 16.4B). As lek size increases, the control of the territorial male over the reproduction of satellites in its court decreases. Territorial males do not evict satellites from their territory but try to prevent them from mating with the female by placing their bill over the satellite’s head in a “mutual squat” that seems to prevent satellites from leaving to mate with females (Hogan-Warburg 1966, van Rhijn 1991, Höglund *et al.* 1993, Hugie and Lank 1997) (Figure 16.4C). If a satellite male is nevertheless seen trying to mate with a female, the territorial male may attack and expel that male from the lek (Hogan-Warburg 1993).

*Philomachus pugnax*, females prefer territories with both territorial and nonterritorial (“satellite”) males, and territorial males actively recruit satellites to their territories by directing displays toward satellites similar to the ones

performed toward females during courtship sequences (Box 16.1). Thus, under some conditions, an increase in female attraction or offspring survival due to the presence of other males seems to overcome the costs of lost fertilizations.

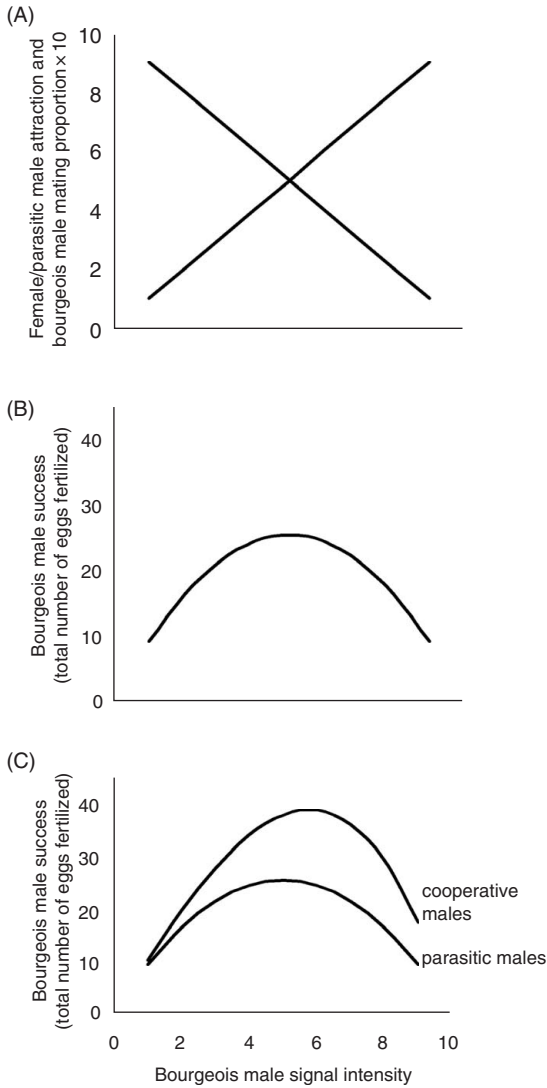


Figure 16.2 (A) Female attraction may increase with the intensity of the bourgeois male sexual signals. Parasitic male attraction may also increase with signal intensity, leading to a decrease in the proportion of fertilizations achieved by the bourgeois male. (B) Bourgeois male sexual signaling intensity should reflect the trade-off between female attraction and mating opportunities lost to parasitic males. (C) The presence of cooperative males may increase the bourgeois male fitness, for example, if the benefits of an increase in female attraction outweigh the costs of lost fertilizations. In these conditions, sexual signals produced by the bourgeois male are expected to increase in conspicuousness. (A) and (B) data from Table 16.1; (C) data from Table 16.2.

Females may also eavesdrop on the bourgeois male sexual signals. Females have been shown to copy the choice of other females in order to select males. Males observed by eavesdropping females being preferred by other females increase in attractiveness (e.g., Dugatkin and Godin 1992); males observed being rejected by females decrease in attractiveness (Witte and Ueding 2003). For example, females of the sailfin molly *Poecilia latipinna* prefer males that they have seen in the presence of other females (e.g., Witte and Ryan 2002) and males observed being rejected by females decrease in attractiveness (Witte and Ueding 2003). It can thus be predicted that bourgeois males should avoid having their signals eavesdropped upon by females when the probability of female rejection is high, but if the probability of female rejection is low, signals should increase in conspicuousness in the presence of female eavesdroppers (Figure 16.5). Bourgeois male sexual signals will therefore be partially shaped by the fitness consequences that eavesdropping imposes on the male, which in turn depends on the nature of the eavesdroppers.

#### RECEIVING BEHAVIOR IN RELATION TO EAVESDROPPING PRESSURE

Eavesdropping is not only expected to influence signal production by bourgeois males but also the way bourgeois males receive and interpret signals. Again, the nature of the eavesdroppers (i.e., females, parasitic males, or cooperative males) will impose different selection pressures on bourgeois males' receiving systems.

The receiving systems of bourgeois males should be selected to detect males using parasitic tactics (e.g., sneakers and female mimics) in order to minimize costs of parasitism. This is likely to be a difficult task as parasitic males are expected to evolve behavioral and morphological adaptations that make such detection difficult. Sneaker males use inconspicuous or darting behavior to avoid detection by bourgeois males. Female mimics imitate female morphology and behavior for the same reason. Thus, an evolutionary arms race between the bourgeois male's detection and discriminatory abilities and the parasitic male's signaling system and reproductive behavior is expected. In other words, the occurrence of eavesdropping by parasitic males in species with ARTs will likely be one of the selection pressures shaping the nature of sensory and perceptive systems of bourgeois males.

Bourgeois males' receiving systems should also be adjusted to detect cooperative males. In the context of ARTs, cooperative males usually pay some price to stay

Table 16.2. *A hypothetical example of variation in female and cooperative male attraction in relation to the intensity of a sexual signal produced by a bourgeois male. Cooperative males that intercept the male signal and move to the bourgeois male territory are assumed to further increase female attraction but also to reproduce parasitically within the territory*

| Signal intensity | No. cooperative males attracted | No. females attracted by the bourgeois male's signal ( $F'$ ) + by the presence of cooperative males ( $F''$ ) <sup>a</sup> | Total number of eggs laid <sup>b</sup> | Total number of eggs fertilized by cooperative males <sup>c</sup> | Proportion of eggs fertilized by the bourgeois male | Total number of eggs fertilized by the bourgeois male |
|------------------|---------------------------------|---|--|---|---|---|
| $I$              | $C$                             | $F' + F'' = F$  | $E = F \times 10$                      | $L = (C \times E) / 10$   | $M = (E - L) / E$                                   | $S = E - L$   |
| 1                | 1                               | 1+0.1=1.1   | 11                                     | 1.1   | 0.9   | 9.9   |
| 2                | 2                               | 2+0.4=2.4   | 24                                     | 4.8   | 0.8   | 19.2  |
| 3                | 3                               | 3+0.9=3.9   | 39                                     | 11.7  | 0.7   | 27.3  |
| 4                | 4                               | 4+1.6=5.6   | 56                                     | 22.4  | 0.6   | 33.6  |
| 5                | 5                               | 5+2.5=7.5   | 75                                     | 37.5  | 0.5   | 37.5  |
| 6                | 6                               | 6+3.6=9.6   | 96                                     | 57.6  | 0.4   | 38.4  |
| 7                | 7                               | 7+4.9=11.9  | 119                                    | 83.3  | 0.3   | 35.7  |
| 8                | 8                               | 8+6.4=14.4  | 144                                    | 115.2   | 0.2   | 28.8  |
| 9                | 9                               | 9+8.1=17.1  | 171                                    | 153.9   | 0.1   | 17.1  |

<sup>a</sup> Assuming females are attracted by cooperative males by  $F'' = C^2/10$ .

<sup>b</sup> Assuming each female lays 10 eggs.

<sup>c</sup> Assuming each cooperative male fertilizes 10% of the eggs.

in the male's territory and to have privileged access to reproductive resources (e.g., Martin and Taborsky 1997, Balshine-Earn *et al.* 1998, Bergmüller *et al.* 2005, Bergmüller and Taborsky 2005). This suggests that bourgeois males are able to individually recognize cooperative males and that cooperative males benefit from this recognition (but see Pfeiffer *et al.* 2005). However, although individual recognition has been demonstrated in several taxa (e.g., invertebrates: Karavanich and Atema 1998; fish: Höjesjö *et al.* 1998; reptiles: Olsson 1994; birds: Whitfield 1987; mammals: Sayigh *et al.* 1999), empirical evidence for direct reciprocity in the context of ARTs is lacking, and examples of reproductive concessions of bourgeois males to cooperative males are rare (Clutton-Brock *et al.* 2001). More likely, in most of these systems, bourgeois males are unable fully to control the reproduction of cooperative males that, once in the territory, may use inconspicuous approaches to access females. As a consequence, most cooperative males still reproduce parasitically. Identifying a cooperative male as such should be an easy task for a bourgeois male as cooperative males should signal their cooperative nature, but detecting parasitic events by these cooperative males is likely to be more difficult. In the ruff, territorial males

adopt a specific behavior that tries to prevent satellite males from accessing females, and satellite males may be expelled from the lek if seen mating (Box 16.1). In the cichlid *Neolamprologus pulcher*, cooperative males detected parasitizing fertilizations were expelled from the group by the breeding pair (Dierkes *et al.* 1999). Thus, the receiving systems of bourgeois males should be selected to detect parasitic events by both cooperative and parasitic males. Hypothetically, this detection may be easier in the case of cooperative males because cooperative males need to advertise their cooperative nature. In many species both cooperative and truly parasitic males occur, providing a good model to test this hypothesis. Also, a comparison of the properties of the bourgeois males' receiving systems in populations with different degrees of prevalence of parasitic males may reveal adaptations to eavesdropping pressure, but no comparative analyses on this issue in the context of ARTs have been conducted to date.

Finally, bourgeois males' receiving systems may also be tuned to eavesdrop on signals produced by other bourgeois males. For example, in the cricket frog *Acris crepitans*, males may either call to attract females or wait in the proximity of calling males and try to intercept approaching females

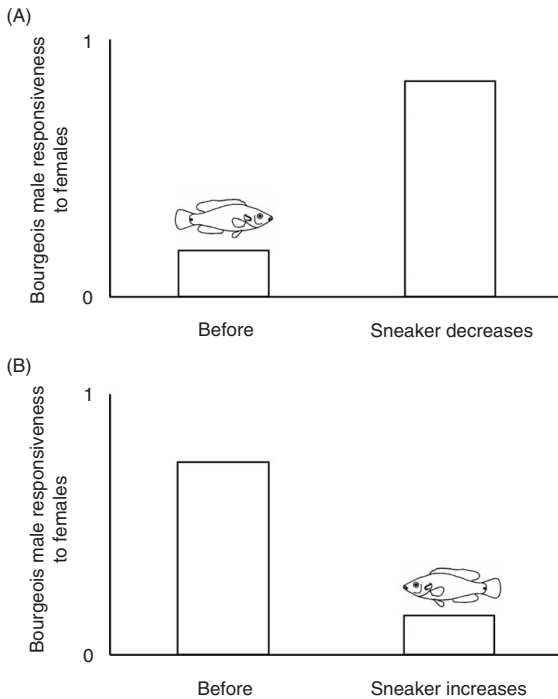


Figure 16.3 In the ocellated wrasse *Symphodus ocellatus*, bourgeois males' success decreases as the number of sneakers around the nest increases. (A) Males increase their courtship displays to females when the number of sneakers is experimentally decreased and (B) decrease their responsiveness to females when sneakers are experimentally increased. (Data from Alonzo and Warner 1999.)

(“satellite males”). Small, calling males, presented with playbacks of low-frequency calls typical of large males, may stop calling and switch into the satellite tactic within minutes (Wagner 1992) (Figure 16.6). The proportion of males switching into the satellite tactic correlates with the decrease in the frequency of the call, that is, with an increase in apparent male size. Thus, bourgeois males may also gain by increasing the probability of detection of signals from other bourgeois males in order to adjust their own signal production and even to switch between reproductive tactics.

### 16.3.2 The parasitic and cooperative male perspectives

#### SIGNALING TO BOURGEOIS MALES AND FEMALES

Cooperative males should signal their cooperative intentions to bourgeois males in order to access reproductive

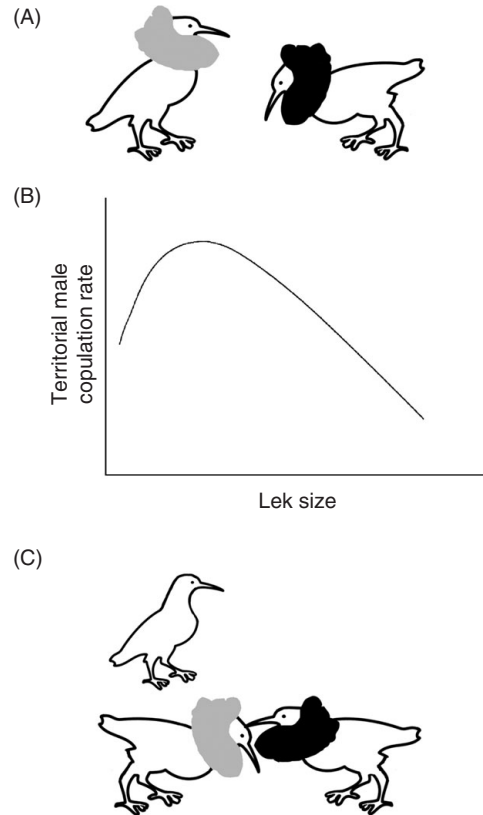


Figure 16.4 In the ruff *Philomachus pugnax*, territorial males (dark neck plumage) seem to actively recruit satellite males (light neck plumage) to their territories (A), displaying the same courtship displays towards satellites as towards females. The territorial male's reproductive success (B) is predicted to be maximum in medium-sized leks. When a female enters the territory (C), the male tries to control the satellite by placing its bill over the satellite's head and preventing access to the female. (Adapted from Hugie and Lank 1997, Widemo and Owens 1999.)

resources. Accordingly, cooperative males usually look distinct both from females and from bourgeois males. For example, satellite males of the ruff have a light plumage distinct from the darker plumage of territorial males (Lank and Dale 2001) (Box 16.1). In another example, in the cooperatively breeding cichlid *Pelvicachromis pulcher*, cooperative males have a yellow coloration whereas bourgeois males have a red coloration (Martin and Taborsky 1997).

Cooperative behavior patterns like nest building or territory defense should be performed within visual range of the bourgeois male because cooperative males not seen helping



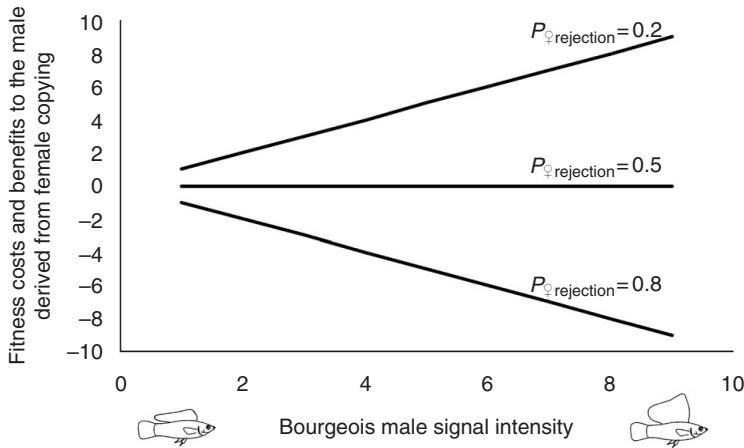


Figure 16.5 Males of the sailfin molly *Poecilia latipinna* observed by eavesdropping females mating with other females increase in attractiveness while rejected males decrease in attractiveness to the eavesdropping females. The intensity of the bourgeois male sexual signals is thus likely to depend on the probability of female rejection

( $P_{\text{♀rejection}}$ ). Successful males that are usually not rejected by females (i.e.,  $P_{\text{♀rejection}} < 0.5$ ) are expected to produce conspicuous signals to benefit from female copying. Unsuccessful males (i.e.,  $P_{\text{♀rejection}} > 0.5$ ) should display less conspicuous signals to avoid having their signals intercepted by eavesdropping females.

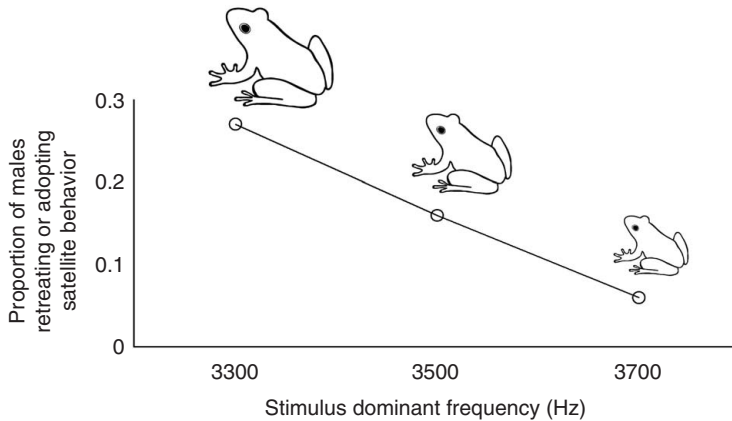


Figure 16.6 Calling males of the cricket frog *Acris crepitans* may switch to a satellite tactic when presented with low-frequency playbacks, typical of large males. More males switch into the

satellite tactic as the frequency of the calls decreases. (Data from Wagner 1992.)

are often attacked by territorial owners (e.g., Balshine-Earn *et al.* 1998). In the cooperatively breeding cichlids *Neolamprologus brichardi* and *N. pulcher* from Lake Tanganyika, helpers compete among themselves for access to positions closer to the brood chamber and helpers close to the nest help more (Werner *et al.* 2003). This investment should be matched by increased access to reproductive resources, either through reproductive concessions by the bourgeois

male or forced access, with more efficient cooperators achieving proportionally higher gains. In these two cichlid species, individuals who help more spend more time inside the brood chamber (Werner *et al.* 2003), potentially having more fertilization opportunities. However, empirical evidence is lacking that helpers in cooperative species with ARTs gain reproductive opportunities in relation to their helping effort. Indeed in *P. pulcher* dominant helpers gain

more parasitic fertilizations than subordinate helpers but their helping rate does not differ (Martin and Taborsky 1997) and in long-tailed tits *Aegithalos caudatus* helping does not relate to shared paternity (Hatchwell *et al.* 2002). This suggests that, at least in some species, cooperative males access the bourgeois male's reproductive resources not by concessions from the bourgeois male but by competing among themselves for access to the best positions for parasitic fertilizations and escaping the bourgeois male's control (Hogan-Warburg 1993, Martin and Taborsky 1997, Werner *et al.* 2003). Cooperating with bourgeois males may allow them to stay in the territory (the "pay-to-stay" hypothesis: e.g., Kokko *et al.* 2002, Bergmüller *et al.* 2005), and once in the territory competition among cooperative males for access to parasitic fertilizations occurs, independently of helping effort. Thus, cooperative males are expected, on the one hand, to develop signals to facilitate transmission of their cooperative intentions to bourgeois males and, on the other hand, to stop signaling and assume sneaking or darting behavior during parasitic events.

Selection should favor parasitic males with adaptations that increase their ability to access reproductive resources without being identified as parasites by bourgeois males and thus they are not expected to advertise their tactic. Parasitic males may rely on small size and speed to quickly access females or nests, or they may mimic females or other bourgeois males. For example, in the shell-brooding cichlid *Lamprologus callipterus*, bourgeois males gather and place shells at the nest entrance that are used by females to lay eggs. During spawning events "dwarf" males make use of their small size (approximately 2.5% the weight of bourgeois males: Sato 1994, Sato *et al.* 2004) to dart quickly inside the shell where a female is spawning and parasitically fertilize eggs from inside the shell (Sato *et al.* 2004). Bourgeois males are too large to enter the shell and evict dwarf males. Thus, dwarf males' success depends on an inconspicuous and fast approach, and both their morphology and behavior are adapted to avoid detection by the bourgeois male.

Males that mimic females in order to participate in mating events are particularly interesting to consider under the framework of communication network theory as they rely on deception to reproduce. Although qualitative observations in several species have suggested that female mimics are indistinguishable from females to the eyes of bourgeois males (e.g., bluegill sunfish *Lepomis macrochirus*: Gross and Charnov 1980, Dominey 1981), only in the peacock blenny *Salaria pavo* has this hypothesis been tested (Gonçalves *et al.* 2005). Bourgeois males of *S. pavo*

sequentially presented with females and female-mimicking males matched for size attacked and courted females and female mimics equally, suggesting that female mimics were able to deceive bourgeois males. However, not all female mimics were equally efficient and larger female mimics were attacked more and courted less by bourgeois males (Gonçalves *et al.* 2005) (Box 16.2). These results may suggest an evolutionary arms race between the female-mimicking signaling mechanisms and the bourgeois males' discrimination systems, with larger female mimics being more easily discriminated by bourgeois males. More generally, the occurrence of female mimics in a population is likely to complicate a bourgeois male's decision to accept or reject a courting conspecific into his nest or territory as it may be a parasitic male instead of a female. Female rejection by bourgeois males is thus likely to increase with the frequency of female mimics in the population.

Female mimicry is also interesting to consider under the scenario of nonindependent mechanisms of choice. Females may eavesdrop on a male-female interaction and copy the choice of other females, for example, to decrease mate-searching costs (e.g., Dugatkin and Godin 1992). When female mimics occur (assuming they also deceive females), females may be observing either a female or a female-like parasitic male courting a bourgeois male. If females still copy the choice of other females in such a system, female mimics may signal to males in the presence of females in order to manipulate female eavesdroppers and increase the probability that mating events will take place in that nest. Interestingly, in the peacock blenny female mimics will perform conspicuous female-like courtship behavior to a bourgeois male even if no spawning event is taking place (D. Gonçalves, personal observations). Whether this is to incite potential eavesdropping females to spawn remains to be tested. In conclusion, signal manipulation by female mimics will certainly be a selection pressure shaping the way other parties communicate in a network.

#### RECEIVING SIGNALS FROM BOURGEOIS MALES AND FEMALES

Parasitic and cooperative males need to locate potential reproductive opportunities. In general, this will be achieved in two steps. First, these males need to locate reproductive areas with high potential for parasitic reproduction and should try to gain a privileged position within those areas. Second, once in reproductive areas these males need to identify and participate in mating events. Locating

**Box 16.2** Sexual dimorphism and courtship

Peacock blennies have pronounced sexual dimorphism with bourgeois males being much larger than females and having a set of well-developed secondary sexual characters, such as a conspicuous head crest (Fishelson 1963, Patzner *et al.* 1986) (Figure 16.7). In a sex-role-reversed population in southern Portugal, females court males using a complex courtship display involving beating the pectoral fins and opening and closing the mouth in synchrony while displaying a typical nuptial coloration (Almada *et al.* 1995). Small males mimic female morphology (Figure 16.7) and complex courtship behavior in order to approach the nest of bourgeois males and release sperm during spawning events (Gonçalves *et al.* 1996). These sneaker males compete for access to the best spawning locations, and successful bourgeois males have more and larger sneakers in the vicinity of their nests (Gonçalves *et al.* 2003a).

Sneakers seem to use both independent and non-independent (i.e., eavesdropping) mechanisms to choose successful males. When given a choice, sneakers prefer to associate with larger nesting males (Gonçalves *et al.* 2003b). Larger males are more frequently courted by females (T. Fagundes, D. Gonçalves, and R. F. Oliveira, unpublished data) and have higher reproductive success (Gonçalves *et al.* 2002); therefore, by associating with large males, sneakers are probably increasing their probability of participating in spawning events. The importance for *S. pavo* sneakers of eavesdropping on sexual interactions to choose successful males was evident in two experiments. Using a copying paradigm, sneakers were shown to prefer to associate with bourgeois males previously seen in the company of females (Gonçalves *et al.* 2003b), and in a second experiment sneakers increased their female-like courtship frequency when observing a female courting a male (R. J. Matos, D. Gonçalves, R. F. Oliveira, and P. K. McGregor, unpublished data). Thus, sneakers are probably using the female's presence and courtship displays as indicators of male quality, and this is likely to correlate with potential opportunities for future parasitic reproduction. It seems plausible that in other systems with ARTs, parasitic males increase their reproductive opportunities both by independent mechanisms of choice and by eavesdropping on the choice of females or even of other parasitic males.

In *S. pavo*, sneakers rely on female mimicry to reproduce. However, bourgeois males should respond by developing good discrimination mechanisms and females by developing a divergent morphology and behavior to signal to nesting males that they are females and not sneakers. The efficiency of female mimicry in *S. pavo* was tested at two levels: a visual model was constructed to estimate how similar sneaker color patterns appear to both females and males and behavioral tests were performed to assess the bourgeois males' behavior towards sneakers and females.

The visual model incorporated visual pigment absorbance and lens transmission data (from White *et al.* 2005), reflectance patterns from several body parts of the three morphs, and ambient light measurements (M. Cummings, D. Gonçalves, and R.F. Oliveira, unpublished data). The model estimated that, for bourgeois males, the color patterns of sneakers and females are much more similar than the color patterns of sneakers and bourgeois males, suggesting that sneakers mimic female colors efficiently. This idea was further tested in a laboratory experiment. Nesting males were sequentially presented with a sneaker and a female matched for size and their aggressive and courtship behavior recorded. Small female mimics were apparently able to deceive bourgeois males, as there was no difference in the amount of courtship and agonistic displays directed by bourgeois males towards small parasitic males or matched-for-size females (Gonçalves *et al.* 2005) (Figure 16.7). However, as body size increased, female mimicry efficiency apparently decreased and sneakers were attacked more and courted less by bourgeois males (Gonçalves *et al.* 2005) (Figure 16.7). An increase in body size may potentially facilitate discrimination by bourgeois males. If this is the case, a large courting female should be more easily correctly identified by the bourgeois male than a smaller one. Larger females were courted more and attacked less than smaller females, although there are alternative explanations for this observation (Gonçalves *et al.* 2005). These results are likely to reflect the conflicts in *S. pavo* derived from the existence of female mimicry. Interestingly, there are differences in the visual sensitivity of sneakers and bourgeois males of *S. pavo* (White *et al.* 2004), raising the possibility that these relate to the different visual tasks alternative reproducing males need to perform.

reproductive areas may not depend on eavesdropping. Parasitic males may, for example, choose to associate with males or reproductive sites that have been previously

preferred by females or to follow reproductively active females until they mate. In the peacock blenny, for instance, both females and sneakers prefer to associate with a large

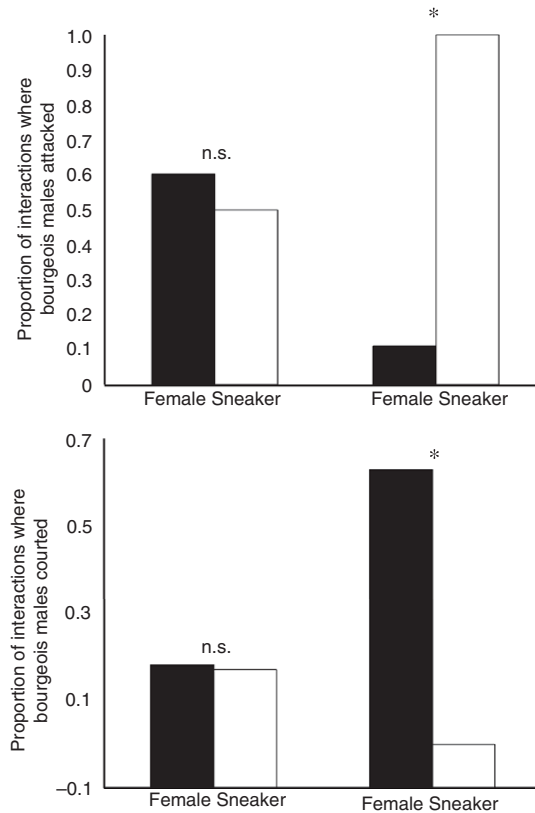


Figure 16.7 In the peacock blenny *Salaria pavo*, small sneaker males mimic the female’s morphology and behavior to approach the nests of bourgeois males. In the field bourgeois males attack and court small sneakers in the same proportion as small females.

Larger sneakers are more attacked and less courted than larger females. Results marked \* are significant at the 0% level; n.s., not significant. (Data from Gonçalves *et al.* 2005.)

male and larger males are more successful in the field (Gonçalves *et al.* 2002, 2003b) (Box 16.2). In another example, male crickets *Acheta domesticus* show phonotaxis for male calls, with small males responding more strongly to playbacks of male calls that are also preferred by females. These small males avoid contact with the speaker, suggesting they eavesdrop on male signals to identify and approach calling males, probably to increase the probability of intercepting females, but avoid direct contact with the larger calling males (Kiflawi and Gray 2000) (Figure 16.8).

Nevertheless, eavesdropping on sexual signals is probably also used widely by parasitic males to locate breeding areas. For instance, sneaker males of *P. notatus* approach a speaker playing back a bourgeois male sexual call, suggesting this signal is used to locate nests (Brantley and Bass 1994, McKibben and Bass 1998, Bass and McKibben 2003). If eavesdropping males locate breeding areas based on

bourgeois male signals, their receiving systems should be well tuned to these signals.

Although there are abundant examples of female sensory systems matching the properties of male calls (e.g., Sisneros and Bass 2003, Sisneros *et al.* 2004), evidence that this is also the case for parasitic and cooperative males is scarce. Nevertheless, sensory differences between male morphs have been identified (e.g., White *et al.* 2004), and this may relate to the different tasks these males need to accomplish. Again, cooperative males would be expected to have good sensory matching to bourgeois male signals as such mechanisms increase the success of the bourgeois male. Bourgeois males may signal directly to cooperative males, as happens in the ruff (van Rhijn 1973, Widemo 1998) (Box 16.1) or include components that facilitate their detection by the receiving system of cooperative males. There are no such advantages to parasitic males; therefore,

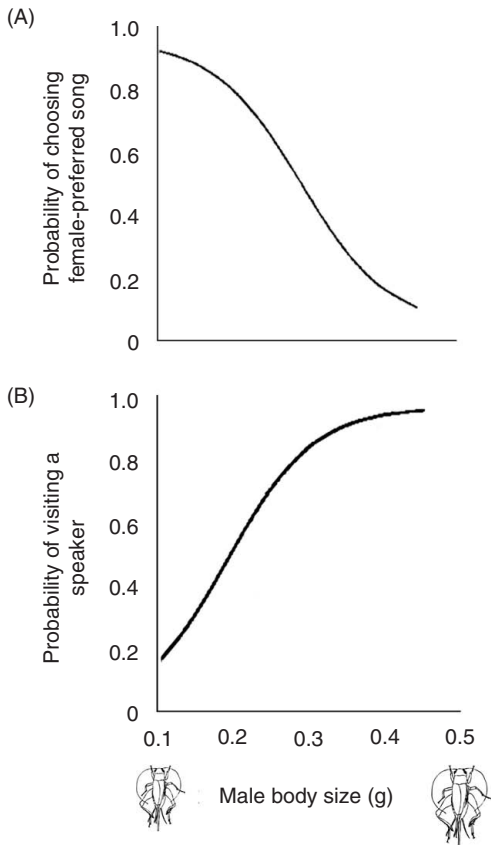


Figure 16.8 In house crickets *Acheta domesticus*, small males (A) show phonotaxis to playback calls of other males preferred by females and (B) avoid contact with the speaker. The results suggest that small males may eavesdrop on calling males' sexual signals to adopt a satellite tactic and intercept females. (Data from Kiflawi and Gray 2000.)

less of a match is expected between the signals of bourgeois males and the receiving systems of parasitic males.

Once in reproductive areas, both cooperative and parasitic males will, on most occasions, try to escape control of the bourgeois male and reproduce parasitically. Eavesdropping on sexual interactions between males and females seems a crucial task for these males as fertilization must, on most occasions, occur during a limited period of time. There is evidence that eavesdropping males pay more attention to sexual signals as a function of parasitic opportunities. For example, in the Mediterranean wrasse the number of sneakers around a nest increases when the bourgeois male courts females more frequently and decreases when the male responsiveness to females decreases (Alonzo and

Warner 1999). In another example, small noncalling males of the grasshopper *Bullacris membracioides* do not respond to playbacks of bourgeois male sexual calls but move towards a speaker playing back a female response call (Donelson and van Staaden 2005). This suggests that these parasitic males are trying to locate and intercept females based on their sexual response calls (Donelson and van Staaden 2005), and the neurophysiology of their auditory system well is adjusted to this task (van Staaden *et al.* 2003). Thus, eavesdropping on sexual signals seems to be ubiquitous in species with ARTs and crucial for the success of both cooperative and parasitic males. Undoubtedly eavesdropping will influence the design of parasitic and cooperative males' receiving systems.

### 16.3.3 The female perspective

#### SIGNALING TO BOURGEOIS, COOPERATIVE, AND PARASITIC MALES

Potentially, females may gain, lose, or suffer no effect by mating with eavesdropping males. The direction of these effects will influence female signaling behavior. Although females are the choosier sex and their sexual signals are less elaborated than in males (except in sex-role-reversed species), females also need to signal their reproductive condition to males and to compete for access to high-quality males. Thus, female signals are also subject to eavesdropping. Whether females will promote or avoid eavesdropping depends on the fitness consequences for the female.

When females benefit from being fertilized by both bourgeois and satellite or parasitic males, they should actively seek multiple-male reproductive situations. For instance, in bluegill sunfish females allow parasitic males to participate in spawning (Gross 1991), in the ruff females seem to prefer to mate in courts co-occupied by satellite and territorial males (Lank and Smith 1992), and in the blue-head wrasse smaller females seek group spawning (Warner 1987, 1990). However, it is unclear in these examples if females actively promote aggregations of males by, for example, signaling both towards bourgeois and parasitic males. Sex-role-reversed species with male ARTs offer a good opportunity to test female preference for distinct male morphs as female courtship behavior is more conspicuous than in species with standard sex roles. In the polygynandrous dunnoek *Prunella modularis*, females solicit copulations equally from dominant alpha males that attempt to guard females and from subordinate beta males (Davies *et al.* 1996). Females increase their solicitation rates towards males who had fewer opportunities to mate (Figure 16.9),

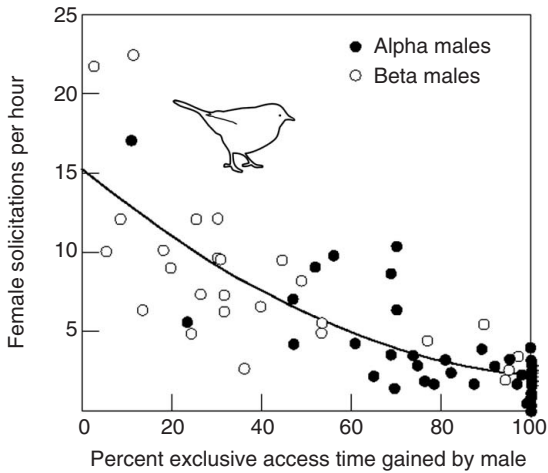


Figure 16.9 In polygynandrous dunnocks *Prunella modularis*, female solicitation rates towards alpha and beta males do not differ and decline with access time gained by the male. (After Davies *et al.* 1996.)

and males invest in parental care in proportion to mating success (Hartley and Davies 1994, Davies *et al.* 1996). Thus, females seem to be maximizing their own reproductive success by manipulating, through sexual signaling, the proportion of shared mating and thus of parental help with alpha and beta males.

In another example, females of the European bitterling fish *Rhodeus sericeus* increase the frequency of conspicuous behavior patterns in the presence of sneaker males prior to spawning, and the participation of sneakers in spawning increases the fertilization success of the eggs (Smith and Reichard 2005). Thus, when females have a net gain by having some of their eggs fertilized by parasitic males, they are expected either to signal directly to these males or to include conspicuous components in their signals to bourgeois males in order to increase the probability of signal interception by eavesdropping parasitic males.

Several alternative explanations have been proposed to explain why females are expected to mate with males of both morphs (e.g., production of offspring from both morphs at the evolutionarily stable strategy frequency if the reproductive strategy is heritable: Henson and Warner 1997, Hugie and Lank 1997, Alonzo and Warner 2000), but a discussion of the reproductive advantages of this and other female mating tactics is beyond the scope of this chapter.

In other species females have been shown to prefer to mate as a pair with bourgeois males. Several hypotheses

have been advanced to explain why females may prefer to mate with bourgeois males; these include gaining both direct benefits (e.g., better paternal care of the eggs) and indirect benefits (e.g., more fit offspring). This seems to be the case in the Mediterranean wrasse *S. ocellatus*, where females apparently choose sneaker-free opportunities to spawn (van den Berghe *et al.* 1989, Alonzo and Warner 2000). In this species, when sneakers are experimentally removed, females increase their spawning rate fourfold, and the nest success may increase threefold (van den Berghe *et al.* 1989, Alonzo and Warner 2000). In these systems, females should avoid parasitic males, and female signals directed to bourgeois males are expected to be conspiratorial. When female mimics occur and impose costs on females, an evolutionary arms race is expected: females should signal to bourgeois males that they are females and parasitic males should counteract with improved female mimicry. This may lead to the evolution of more complex female displays or behavior that are increasingly difficult to mimic. As an example, in the sex-role-reversed population of the peacock blenny described above, females produce a complex courtship display that sneakers imitate. Small sneakers are better at deceiving bourgeois males, presumably because an increase in target area facilitates discrimination (Gonçalves *et al.* 2005) (Box 16.2). These results are likely to reflect an evolutionary arms race where females try to advertise their sex to bourgeois males, female mimics try to deceive bourgeois males, and bourgeois males try to discriminate females from female mimics.

In species where females would prefer to mate with parasitic rather than bourgeois males, female signals should be conspiratorial and directed to parasitic males. In some species females may gain genetic benefits from mating with parasitic males. For example, both in bluegill sunfish and in the Atlantic salmon *Salmo salar* fry from eggs fertilized by sneakers grow faster when compared with fry from eggs fertilized by bourgeois males (Garant *et al.* 2002, Neff 2004). In coho salmon *Oncorhynchus kisutch*, there is some evidence that females prefer to mate with parasitic males and only mate with larger bourgeois males to avoid the costs of coercion (Watters 2005). Thus, the traditional view that females, when given a choice, prefer to mate with bourgeois rather than parasitic males may prove incorrect for some species. In the context of communication networks, this means another level needs to be considered, with possible cooperation during sexual interactions between females and parasitic males and conflict between bourgeois males and both females and parasitic males.

RECEIVING SIGNALS FROM BOURGEOIS,  
COOPERATIVE, AND PARASITIC MALES

Since selection favors females that maximize their long-term reproductive success in mate-choice decisions, females should be tuned to male signals and selected to evaluate male quality from the properties of the signal. For instance, female gray treefrogs *Hyla versicolor* prefer male calls of longer duration (Klump and Gerhardt 1987), and the progeny of “long-callers” are more fit, thus providing females with indirect fitness benefits (Welch *et al.* 1998). In species with ARTs, cooperative and parasitic males eavesdrop on male–female interactions; therefore, a female’s decision to respond to appropriate bourgeois male signals should incorporate the reproductive consequences for her of mating with these eavesdropping males. Females’ receiving systems should thus be tuned not only for the detection and evaluation of bourgeois males’ signals but also for the detection of potential eavesdropping males. Again, identification of cooperative males should be easier than detection of parasitic males as the former usually have distinctive traits to signal their cooperative nature. Discrimination of parasitic males by females’ receiving systems should also be facilitated when females gain from their presence. In this scenario, females and parasitic males may signal to each other in order to increase the probability of mating, and bourgeois males may eavesdrop on this interaction, reducing the conspicuousness of the signal. This hypothesis raises again the interesting possibility that the receiving systems of reproductive morphs within the same population may differ according to their position in the communication network. In this example, females may be better tuned to parasitic male signals than bourgeois males.

In species where females pay a fitness cost by mating with parasitic males, their receiving system should also be selected to identify these males in order to avoid parasitic fertilizations. In this scenario, however, parasitic males are expected to counteract with strategies that decrease their detection by females.

In both situations, females are expected to gain an advantage by discriminating parasitic or cooperative males from bourgeois males. In the first case, discrimination would allow females to select multiple male mating scenarios or to choose parasitic males, and in the second case it would allow females to avoid these males. Female discrimination of alternative morphs seems evident in many species. Female swordtails *Xiphophorus nigrensis*, for example, clearly avoid small males, preferring to mate with larger courting males (for a review see Ryan and Rosenthal 2001). Parasitic males

may counteract, reproducing by forced copulations (e.g., swordtails), fast access to the female (e.g., ruff), or female mimicry (e.g., peacock blenny). It is unclear if female mimics are also able to deceive females.

16.4 INTEGRATIVE APPROACH AND  
FUTURE DIRECTIONS

Game-theoretical models have shown that eavesdropping will influence the way animals communicate (e.g., Johnstone 2000, 2001). Species with ARTs are no exception and, as explained in the previous section, the properties of signaling and receiving systems of bourgeois males, females, parasitic and cooperative males will be influenced by the complex communication network in which animals live. Functional approaches to the study of animal communication in these species will thus need to consider the costs and benefits imposed by eavesdropping on each member of a communication network.

Alternative morphs play different roles in their communication network, and thus different evolutionary pressures act on their signaling and receiving systems. The often dramatic difference in traits between males reproducing using alternative tactics is an obvious consequence of these pressures. The hypothesis that alternative morphs also show differences in their receiving and signaling systems in relation to their particular mode of reproduction has been less explored. For instance, while bourgeois males need to detect females, parasitic males may reproduce by intercepting bourgeois males’ signals. Differences in the sensory and receiving apparatus of alternative morphotypes relating to the distinct roles they play in the communication network are likely to be widespread.

Surprisingly, although research has revealed a plasticity in signal production in relation to eavesdropping pressure, as shown by some of the above examples, a demonstration that eavesdropping influences the evolution of signals in species with ARTs is still lacking. For this, inter- and intraspecific comparative approaches may prove particularly successful, as has been the case in other communication systems. For example, John Endler’s work with guppies *Poecilia reticulata* has demonstrated that the male courtship coloration correlates negatively with predation pressure (Endler 1977, 1978, 1980). Furthermore, in populations with stronger predation pressure, male guppies show a lower frequency of sigmoid displays towards females and a higher frequency of forced copulation attempts, presumably because sigmoid displays are more conspicuous to predators relying

on interceptive eavesdropping (Luyten and Liley 1985, Endler 1987, Magurran and Seghers 1990). Similar comparative approaches could be carried out in species with ARTs where the degree of eavesdropping pressure varies between populations. For example, in the peacock blenny several populations with ARTs have been described. In two populations, a scarcity of nest sites leading to a strong male–male competition for nests is likely to explain the presence of sneakers (Ruchon *et al.* 1995, Gonçalves *et al.* 1996). In other populations, nest-site availability is higher (e.g., in the Adriatic) and the frequency of sneakers in the population is lower (J. Saraiva and R. F. Oliveira, unpublished data). Qualitative observations suggest that in this population male courtship signals are more conspicuous, although it is unclear if this is a consequence of a lower eavesdropping pressure (J. Saraiva and R. F. Oliveira, unpublished data).

Interspecific comparative analyses on the signaling properties of species with ARTs under different eavesdropping pressure may also prove rewarding. By including species with and without ARTs while controlling for phylogeny, one could test whether the properties of signals would change in a predictable way with eavesdropping pressure. For example, when eavesdroppers impose a cost on bourgeois males, one of the predictions would be that bourgeois male sexual signals should include shorter-range components when eavesdropping pressures increase. When female mimics occur, the rate of female rejection by bourgeois males may increase with the frequency of female mimics in the population.

Finally, understanding the output of the complex interaction between and within the sexes in species with ARTs is only likely to be possible with a combination of experimental and observational work aided by mathematical models. A full understanding of animal communication in these systems will necessarily include measuring the fitness consequences of signal production and reception for bourgeois males, females, parasitic and cooperative males and combining these results in holistic models.

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