

Male Topi Antelopes Alarm Snort Deceptively to Retain Females for Mating

Jakob Bro-Jørgensen^{1,*} and Wiline M. Pangle²

1. Mammalian Behaviour and Evolution Group, Faculty of Health and Life Sciences, Leahurst Campus, University of Liverpool, Neston CH64 7TE, United Kingdom; and Institute of Zoology, Zoological Society of London, London NW1 4RY, United Kingdom;

2. Department of Evolution, Ecology and Organismal Biology, Ohio State University, Columbus, Ohio 43210

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ABSTRACT: Despite intense interest in the role of deception in animal communication, empirical evidence is wanting that nonhuman animals are capable of actively falsifying signals to manipulate mates for reproductive benefits. Tactical use of false positive signals has thus been documented mainly where interests are consistently opposed, such as between predator and prey and between competitors for food and for mates. Here we report that male topi antelopes alarm snort deceptively to retain receptive females in their territories and thereby secure mating opportunities. The finding reveals that sexual conflict over mating, which is known to promote various forms of coercion and sensory bias exploitation, can also lead to active signal falsification. However, because honesty in sexual signals is generally assured by physical or cost-enforced constraints on signal production, sexually selected mate deception is likely to target mainly signals, such as alarm calls, that were originally not under sexual selection.

Keywords: sexual selection, sperm competition, sexual conflict, deception.

Introduction

While early theoretical work focused on mechanisms that maintain honesty in animal communication (Enquist 1985; Grafen 1990), more realistic models have since emphasized that deception can constitute part of otherwise honest signaling systems, provided that benefits of reacting to true signals outweigh costs of reacting to false signals (Johnstone and Grafen 1993; Rowell et al. 2006). Still, empirical evidence of deception is extraordinarily rare, particularly when it comes to tactical deception (i.e., “acts from the normal repertoire of the agent, deployed such that another individual is likely to misinterpret what the acts signify, to the advantage of the agent”; Byrne and Corp 2004, p. 1695). Tactical deception has been documented

from contexts where the interests of individuals are consistently opposed. For example, deception of predators underlies the “broken wing display,” where the plover *Charadrius* spp. leads intruders away from its nests by feigning injury (Ristau 1991). Other examples involve falsification of signals (Caldwell 1986; Plath et al. 2008; Whiting et al. 2009), and here, alarm calls appear to be particularly prone to exploitation. For example, false alarms are used by certain bird species to scatter competitors away from food sources (Matsuoka 1980; Munn 1986; Møller 1988) and possibly also by male vervet monkeys *Cercopithecus aethiops* to disrupt intergroup encounters (Cheney and Seyfarth 1990). Sexual rivals may be manipulated by false alarms as well; for example, chimpanzees *Pan troglodytes* are reported to use false alarm calls to distract the attention of conspecifics and thereby gain access not only to desired objects but also to mates (de Waal 1986; Miles 1986). However, when it comes to communication between sexual partners, who share the common goal of reproduction, the scope for evolution of tactical deception is controversial, particularly in regard to active falsification of signals. Males use false alarms to disrupt extrapair copulations in swallows (Møller 1990) and to render conspecifics immobile after copulation in squirrels (Tamura 1995); however, it is unclear whether the advantage in emitting false alarms in these cases lies in their effect on the female or rather on the sexual rivals.

Here, we report that false alarm snorts are used by male topi antelopes (*Damaliscus lunatus*) to tactically deceive receptive females who intend to leave a male's territory into believing that they are headed toward a predator. Consequentially, the departure of the female is delayed, providing the male with additional mating opportunities. The finding points to intentional deception of sexual partners as a potentially important outcome of sexual conflicts in nonhuman animals.

* Corresponding author; e-mail: bro@liv.ac.uk.

Predictions

To investigate why topi males occasionally alarm snort in the absence of danger, we tested a set of predictions arising from two alternative hypotheses, that is, the “sexual deception hypothesis,” which suggests that males use false alarms to prevent the departure of receptive females from mating territories, and the “error hypothesis,” which suggests that false alarms are mistakes. First, both hypotheses predict that false alarm snorts will be indistinguishable from true snorts in their acoustic structure. According to the sexual deception hypothesis, we furthermore predicted that (1) false snorts would be associated with the presence of receptive females in the male territory, and specifically with departure attempts of such females; (2) females would respond to false snorts by delaying their departure from the territory of the snorting male; and (3) males would have a nontrivial probability of siring after emitting false snorts. According to the error hypothesis, we expected that because false alarms occurred only in the presence of conspecifics, the primary function of true alarms would be to warn conspecifics rather than to signal detection to the predator in order to deter pursuit.

Methods

Study Population

We studied topi, a medium-sized, gregarious savanna antelope, in the Masai Mara National Reserve, Kenya (1°15′–1°43′S, 34°47′–35°24′E), between 2005 and 2009. In the study area, the topi rut typically lasts approximately 1.5 months, with a variable onset between February and March. At this time, most adult males defend individual mating territories whose size averages 14.3 ha (SEM = 1.7; range: 0.2–119.1 ha; $n = 150$ territories). Herds of nonterritorial females roam over the territorial mosaic, and during a female’s 1-day estrus (Estes 1991), she visits multiple male territories (average 10; J. Bro-Jørgensen, unpublished data) and mates repeatedly (average 11 times) with several of the territory holders (average 4; Bro-Jørgensen 2007).

Alarm snorts are emitted by both sexes when they detect stalking predators (Estes 1991), notably lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), leopards (*Panthera pardus*), and humans (*Homo sapiens*; Sinclair et al. 2003). While emitting the snorts, the topi stare at the predator with their ears pricked. The topi thereby prevent stalkers, who are unable to outrun topi over longer distances, from approaching close enough to launch a successful attack (Sherman 1977).

Focal Watches

During the rut, 53 estrous and 20 nonestrous females were watched focally for a total of 274 h. Individuals were identified from natural marks, and estrus in females was detected from male behavior (Bro-Jørgensen 2007). During the focal watches, we recorded the territorial location of the focal female, female numbers in the territory, all matings (defined by intromission), all alarm snorts by the territorial male, and all attempted female territory shifts (categorized into “successful” or “prevented by male herding”). Following alarm snorts, we scanned the area thoroughly for the presence of any predators, which was possible due to the open habitat and the topi’s habit of keeping predators in sight. On this basis, alarm snorts were categorized as true or false. All observations were done from a Toyota four-wheel-drive car to which the topi were habituated.

Acoustic Analyses

Topi vocalizations were recorded using a solid-state recorder (Marantz PMD670) with a directional microphone (Sennheiser ME 67). Focusing on 21 males who were recorded emitting both true and false alarms, we analyzed an average of 9 snorts per male (range: 4–22) using Praat 5.0.42 (P. Boersma and D. Weenink, University of Amsterdam). The duration of snorts was measured in narrow-band spectrograms generated by fast Fourier transformation (window length = 0.025 s, time step = 1,000, frequency step = 250, bandwidth = 52 Hz, Gaussian window shape, dynamic range = 50 dB), and the dominant frequency was measured in power spectra.

Playback Experiment

We conducted a playback experiment to determine whether females respond to false alarms in a manner that delays their departure from the male’s territory. We broadcast three types of male vocalizations to grazing females, namely, the true and false male alarm snorts and, as a control, a grunt that is a nonalarm vocalization produced by territorial males (Estes 1991). These three vocalizations were broadcast 20 times each to a total of 60 randomly chosen grazing females from 35 m away (measured by a Bushnell Yardage Pro 800 laser range finder). Individual recordings were played back only twice on average to avoid pseudoreplication, and no topi received a playback stimulus more than once, to avoid habituation (McGregor et al. 1992). Playback volume was calibrated to natural levels using a Creative Nomad Jukebox 3 with two loudspeakers (Fender Passport P-150) spaced 20 cm apart on car window mounts facing away from the focal animal and hidden

by the car. Female reactions were recorded for later analysis using a digital video camera (Sony DCR-H65). The distance covered by females who reacted by walking was estimated by multiplying the duration of walking by the average female walking speed of $0.98 \pm 0.02 \text{ m s}^{-1}$ (mean \pm SEM; $n = 20$ females); the average female walking speed was calculated by using the laser range finder to measure the distance covered by undisturbed females walking directly away from the car and dividing by the corresponding duration (average 51 s).

Threat Exposure Experiment

Because false alarms were produced only in the presence of conspecifics, we assumed that if false alarms were mistakes then the primary function of true alarms would be to communicate to conspecifics rather than the predator. Alarm snorts may indeed function as warnings to conspecifics, in which case the signaler can benefit from kin selection, if receivers are close relatives (Hamilton 1964; Sherman 1977), and/or from reciprocity, if receivers become more inclined to warn the signaler in the future (Trivers 1971). However, alarm snorts may also signal detection to the predator in order to deter further pursuit (Sherman 1977). Only the last hypothesis clearly predicts that solitary individuals will alarm snort in the face of danger. To test this prediction we recorded the response of solitary male topi to a human approaching on foot from 40 m away. Snorts emitted in this context were assumed not to function in intraspecific communication.

Statistical Analyses

All statistical analyses were two tailed, and they were performed in SPSS/PASW, version 17.0.2.

Results and Discussion

In our acoustic analyses, we detected no systematic differences between true and false alarms in either their duration ($222 \pm 4 \text{ ms}$; Wilcoxon: $Z = -0.087$, $P = .931$) or their dominant frequency ($2,028 \pm 28 \text{ Hz}$, $Z = -1.03$, $P = .305$; $n_1 = n_2 = 21$ males; fig. 1; audio file 1 in the online edition of the *American Naturalist*). In support of the idea that males target the false alarms at receptive females, we found that males almost exclusively emitted the false snorts when one of the females in their territory was in estrus. Thus, a focal female would have a significantly higher probability of hearing a false snort during a territorial visit when she was in estrus than not ($0.25 \text{ vs. } <0.01$; Mann-Whitney: $Z = -6.59$, $P < .001$). This was in spite of estrous females being in generally smaller herds ($Z = -2.25$, $P = .024$) and estrus state having no signifi-

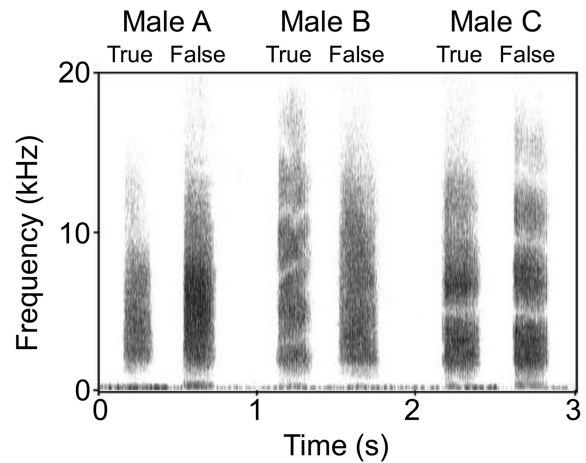


Figure 1: A narrow-band spectrogram of true and false alarm snorts from three individuals (window length = 0.025 s, bandwidth = 52 Hz, Gaussian window shape). The examples are available in audio file 1 (WAV; 300 kB) in the online edition of the *American Naturalist*, where they occur in the same order (i.e., alternating true and false alarm snorts in this sequence: male A true, male A false, male B true, male B false, male C true, male C false).

cant effect on visit duration in the sample (average 42 min; $Z = -1.06$, $P = .287$; $n_1 = 20$ nonestrous females, $n_2 = 53$ estrous females). Furthermore, supporting that the function of the snorts is to delay the departure of the receptive female, we found a clear positive link between departure attempts, successful or not, by estrous females and the onset of the false snorts, 3 min being the median interval between the two events (fig. 2A; table 1). When emitting the false snorts, the male characteristically was standing in front of the female, alert and with ears pricked while staring in the direction that she was heading, exactly as if a predator had been detected in front (fig. 3A).

In the playback experiment, we found that the alarm snorts elicited significantly stronger reactions than the control, with no detectable difference between true and false alarms (fig. 2B). Hence, while both types of alarms invariably caused females to raise their heads and look toward the hidden loudspeakers, grunts elicited this response in fewer than half of the cases (45%; Kruskal-Wallis: $\chi^2_2 = 26.49$, $P < .001$; one-way ANOVA comparing latency to resuming grazing: $F_{2,57} = 7.11$, $P = .002$; Tukey HSD post hoc comparisons: control vs. true alarm $P = .007$, control vs. false alarm $P = .004$, true vs. false alarm $P = .985$). Females reacted to the playback of snorts by walking away from the speakers in 43% of the cases, after standing vigilant for an average of $20 \pm 3 \text{ s}$ (Kruskal-Wallis: $\chi^2_2 = 12.75$, $P = .002$; no difference between true and false snorts in response frequency, $\chi^2_1 = 0.898$, $P = .343$; latency to walking, t -test: $t_{15} = -0.295$, $P = .772$;

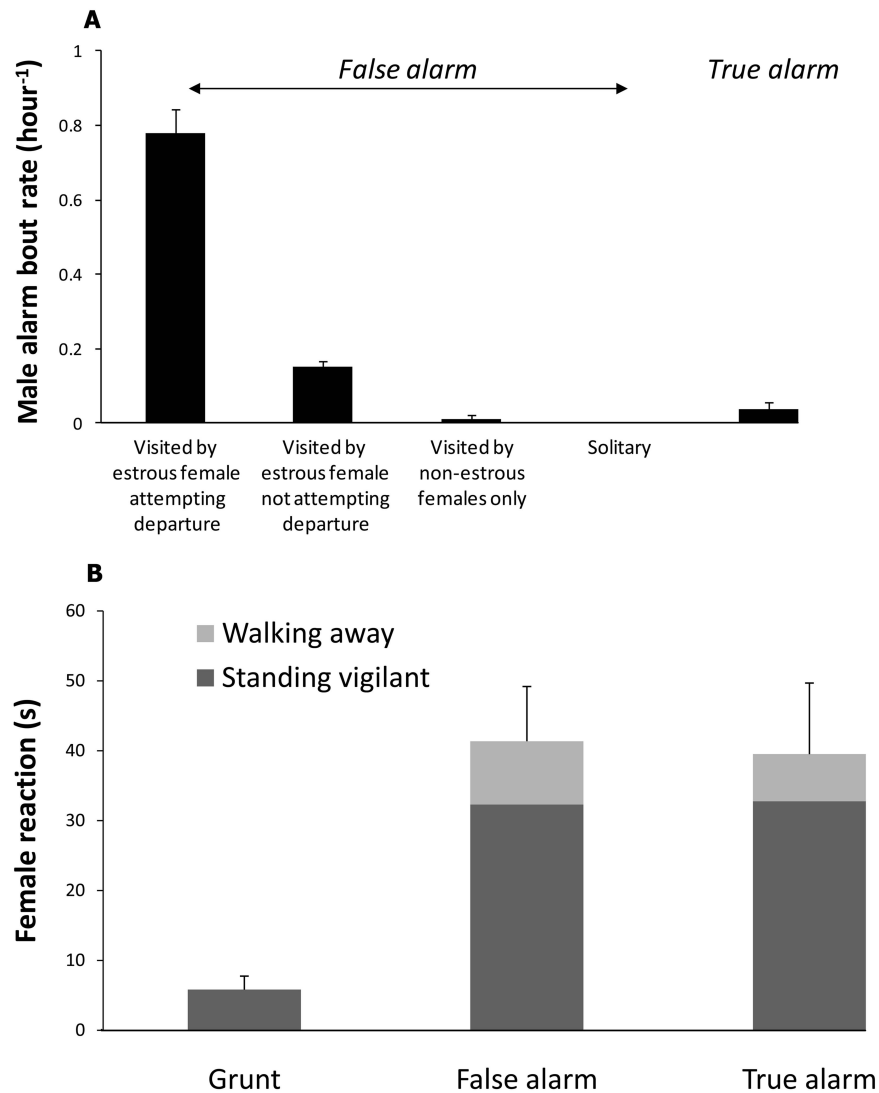


Figure 2: Male alarm bout rates and female reactions. *A*, Rates of alarm bouts from territorial males. For false alarms, separate rates are shown for when the male is visited by an estrous female, with the quartile of the visit closest to departure attempts of the female shown separately from the remainder of the visit (i); when visited by nonestrous females only (ii); and when alone (iii). Also shown is the rate of true alarm bouts. Columns and error bars denote mean \pm SEM for 15 males in each category. Successive alarm snorts by a male in the same situation are defined as a bout. *B*, Female reactions to playback of three male vocalizations: grunts (as control) and false and true alarm snorts. Columns represent the means for 20 females in each category, with error bars denoting SEM for the duration of the total response (i.e., the “walking away” and “standing vigilant” responses added together).

or duration of walking, $t_{38} = -0.602$, $P = .551$). We presume that this walk-away response is a precaution that allows for the possibility that an undetected predator is present after all. Because males generally produce the false snorts from a position between the target female and their territorial boundary, the walk-away response typically brings the female back toward the interior of the snorting male’s territory under natural conditions. Hence, the distance covered by the walk-away response, which averaged

18 ± 3 m, is generally well below the width of the male territory.

Males secure additional mating opportunities by retaining estrous females in their territories, achieving on average 2.8 ± 0.6 intromissions in the interval between the onset of their false alarm snorts and the female’s eventual departure ($n = 56$ males). In 10% of the visits with false snorts, the male succeeded in mating only after he had begun snorting, and in these cases the benefits from

Table 1: Logistic regression model predicting the onset of false male alarm snorts during a visit by an estrous female

| Variable | Coefficient (<i>B</i>) | χ^2 | df | <i>P</i> |
|--|--------------------------|----------|----|----------|
| Time to attempted departure of the female (log [$x + 1$], min) | -1.028 | 19.44 | 1 | <.001 |
| Duration of the female visit (log, min) | -1.699 | 271.68 | 1 | <.001 |
| Number of females in the territory (log) | ... | .330 | 1 | .566 |
| Whether the departure attempt successful | ... | .124 | 2 | .940 |
| Female ID | ... | 3.034 | 53 | 1.00 |
| Male ID | ... | 2.852 | 56 | 1.00 |
| Intercept | ... | .124 | 1 | .725 |

Note: Based on 103 territorial visits during which the male emitted false alarm snorts; total duration was 73 h. The final model ($\chi^2 = 5,245$, $df = 2$, $P < .001$) was obtained by backward stepwise regression and included only significant terms ($P < .05$); results relating to nonsignificant variables were obtained through their separate addition to the final model.

the manipulation are likely to be particularly high. It indeed appeared that false alarms were tactically linked to mating, since males often attempted to mate shortly after emitting a false snort (fig. 3B, 3C; video 1 in the online edition of the *American Naturalist*). The false alarms may further serve a mate-guarding function. Hence, because a male on average would have mated 4.3 ± 0.7 times with an estrous female before his first false snort ($n = 56$ males), delaying the female's departure, even without further mating, can entail benefits by preventing subsequent matings with other males and thereby reducing the intensity of sperm competition (Simmons 2001). Although data are not available from topi, it is known from other promiscuous bovids that a male's siring probability increases with his proportion of the total number of sperm in the female reproductive tract (Dziuk 1996).

The result of our threat exposure experiment was also more consistent with the sexual deception hypothesis than with the error hypothesis. We found that solitary males invariably snorted when approached by a human on foot (latency to first snort: 38.4 ± 6.4 s [2–120 s]; $n = 20$ males). This suggests that true alarms function primarily as pursuit deterrents aimed at predators rather than as warnings to conspecifics. In contrast, the false alarms were emitted specifically when territorial males were visited by females (association between female presence and false alarm snort bouts in a sample of 68 territorial males: $\chi^2_1 = 13.0$, $P < .001$), and it is not obvious why errors would be limited to this context.

Our findings thus point to the false alarm snort in topi as a manipulative trait in a sexual conflict over mating rates (Hosken and Stockley 2005; Lessells 2006). Such conflicts have been shown to promote various forms of coercion and sensory bias exploitation (Arnqvist and Rowe

2005; Lessells 2006); however, that adaptations to mating conflicts can also lead to active signal falsification is a novel discovery. In the present case, females appear unable to distinguish true snorts from false snorts acoustically, and males are therefore likely to have an advantage in the sexual conflict: they incur only low costs from producing false snorts while female resistance, that is, ignoring snorts, can lead to extremely high costs, namely death. Indeed, the importance of detecting predators in the study system is underscored by the finding that the topi population in the study area is limited by predation rather than food (Sinclair et al. 2003). Also, the benefits of winning the conflict are likely to be greater for males than females. Hence, while males by their manipulation might increase offspring number, females probably gain more modest benefits by ignoring false snorts: depending on whether their attempted territory shift is motivated by resource availability or mate preferences (Bro-Jørgensen 2002), the females may temporarily improve foraging or potentially enhance the quality (rather than the quantity) of their offspring. That males have the upper hand in the conflict is supported by the observation that males emitted as many as nine false alarm snorts for every true snort when visited by estrous females (J. Bro-Jørgensen and W. M. Pangle, unpublished data). This high frequency of false snorts may seem surprising; however, females experience this high ratio of dishonesty only during their 1-day estrus or if in the vicinity of another estrous female in a male territory.

The demonstration that topi have the behavioral flexibility to actively falsify signals in order to deceive mating partners reveals a broader scope for tactical deception in animals than is currently appreciated. Such infiltration of established communication systems by deception is likely to be most common in signals that are not sexually selected

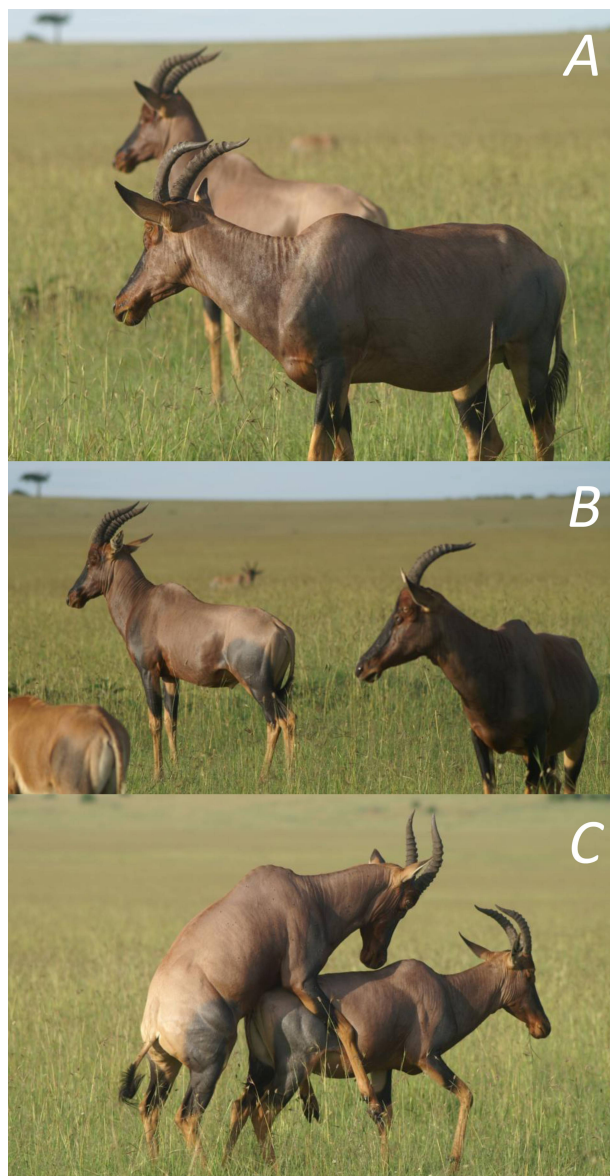


Figure 3: Deceptive use of alarm snorts. *A*, A topi male (*in background*) has just emitted a false alarm snort close to the boundary of his territory and stares into the distance as if a stalking predator has been detected. A receptive female (*in foreground*) who was heading toward the alleged danger stops and looks ahead alertly. *B*, As she turns to move away, the male quickly shifts his attention toward the female, as revealed by the change in the orientation of his ears and his gaze. *C*, Shortly afterward the male succeeds in mating with the female. Another example of a male obtaining matings after false snorts is shown in video 1 (MPEG; 16 MB) in the online edition of the *American Naturalist*.

in origin. This is because sexually selected signals often are either too costly to fake or mechanically impossible to fake (Searcy and Nowicki 2005). Among nonsexually selected signals, alarm calls may be particularly prone to

manipulation because they relatively easily fulfill the prerequisite that the costs of reacting to false signals must be outweighed by benefits of reacting to true signals. Although firm statements about intentions behind behaviors are notoriously difficult to make, our study does identify a parallel between animals and humans in their capability of using false signaling to deceive mates, a finding that hints that their communication may be less fundamentally different than widely assumed (Premack 2007).

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Literature Cited

- Arnqvist, G., and L. Rowe. 2005. *Sexual conflict*. Princeton University Press, Princeton, NJ.
- Bro-Jørgensen, J. 2002. Overt female mate competition and preference for central males in a lekking antelope. *Proceedings of the National Academy of Sciences of the USA* 99:9290–9293.
- . 2007. Reversed sexual conflict in a promiscuous antelope. *Current Biology* 17:2157–2161.
- Byrne, R. W., and N. Corp. 2004. Neocortex size predicts deception rate in primates. *Proceedings of the Royal Society B: Biological Sciences* 271:1693–1699.
- Caldwell, R. L. 1986. The deceptive use of reputation by stomatopods. Pages 129–145 in R. W. Mitchell and N. S. Thomson, eds. *Deception: perspectives on human and nonhuman deceit*. SUNY Press, Albany.
- Cheney, D. L., and R. M. Seyfarth 1990. *How monkeys see the world: inside the mind of another species*. University of Chicago Press, Chicago.
- de Waal, F. 1986. Deception in the natural communication of chimpanzees. Pages 221–244 in R. W. Mitchell and N. S. Thomson, eds. *Deception: perspectives on human and nonhuman deceit*. SUNY Press, Albany.
- Dziuk, P. J. 1996. Factors that influence the proportion of offspring sired by a male following heterospermic insemination. *Animal Reproduction Science* 43:65–88.
- Enquist, M. 1985. Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Animal Behaviour* 33:1152–1161.
- Estes, R. D. 1991. *The behavior guide to African mammals*. University of California Press, Berkeley.

- Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology* 144:517–546.
- Hamilton, W. D. 1964. Genetical evolution of social behaviour. I. *Journal of Theoretical Biology* 7:1–16.
- Hosken, D. J., and P. Stockley. 2005. Sexual conflict. *Current Biology* 15:R535–R536.
- Johnstone, R. A., and A. Grafen. 1993. Dishonesty and the handicap principle. *Animal Behaviour* 46:759–764.
- Lessells, C. M. 2006. The evolutionary outcome of sexual conflict. *Philosophical Transactions of the Royal Society B: Biological Sciences* 361:301–317.
- Matsuoka, S. 1980. Pseudo warning call in titmice. *Tori* 29:87–90.
- McGregor, P. K., C. K. Catchpole, T. Dabelsteen, J. B. Falls, L. Fusani, H. C. Gerhardt, F. Gilbert, et al. 1992. Design of playback experiments: the Thornbridge Hall NATO ARW Consensus. Pages 1–9 in P. K. McGregor, ed. *Playback and studies of animal communication*. Plenum, New York.
- Miles, H. L. 1986. How can I tell a lie? apes, language, and the problem of deception. Pages 245–266 in R. W. Mitchell and N. S. Thomson, eds. *Deception: perspectives on human and nonhuman deceit*. SUNY Press, Albany.
- Møller, A. P. 1988. False alarm calls as a means of resource usurpation in the great tit *Parus major*. *Ethology* 79:25–30.
- . 1990. Deceptive use of alarm calls by male swallows, *Hirundo rustica*: a new paternity guard. *Behavioral Ecology* 1:1–6.
- Munn, C. A. 1986. Birds that cry wolf. *Nature* 319:143–145.
- Plath, M., S. Richter, R. Tiedemann, and I. Schlupp. 2008. Male fish deceive competitors about mating preferences. *Current Biology* 18:1138–1141.
- Premack, D. 2007. Human and animal cognition: continuity and discontinuity. *Proceedings of the National Academy of Sciences of the USA* 104:13861–13867.
- Ristau, C. A. 1991. Before mindreading: attention, purposes and deception in birds? Pages 209–222 in A. Whiten, ed. *Natural theories of mind*. Blackwell, Oxford.
- Rowell, J. T., S. P. Ellner, and H. K. Reeve. 2006. Why animals lie: how dishonesty and belief can coexist in a signaling system. *American Naturalist* 168:E180–E204.
- Searcy, W. A., and S. Nowicki. 2005. *The evolution of animal communication*. Princeton University Press, Princeton, NJ.
- Sherman, P. W. 1977. Nepotism and the evolution of alarm calls. *Science* 197:1246–1253.
- Simmons, L. W. 2001. *Sperm competition and its evolutionary consequences in the insects*. Princeton University Press, Princeton, NJ.
- Sinclair, A. R. E., S. Mduma, and J. S. Brashares. 2003. Patterns of predation in a diverse predator-prey system. *Nature* 425:288–290.
- Tamura, N. 1995. Postcopulatory mate guarding by vocalization in the Formosan squirrel. *Behavioral Ecology and Sociobiology* 36:377–386.
- Trivers, R. L. 1971. Evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–57.
- Whiting, M. J., J. K. Webb, and J. S. Keogh. 2009. Flat lizard female mimics use sexual deception in visual but not chemical signals. *Proceedings of the Royal Society B: Biological Sciences* 276:1585–1591.

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Topi on a termite hill in the Masai Mara National Reserve, Kenya. Photograph by Jakob Bro-Jørgensen.