



Why hide? Concealed sex in dominant Arabian babblers (*Turdoides squamiceps*) in the wild

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ABSTRACT

Striking uniformity exists in humans' preference to conceal sexual activity from conspecifics' view. Yet, little is known about the selective pressures acting upon its evolution. To investigate this question, we studied the cooperatively breeding Arabian babbler (*Turdoides squamiceps*), which has been suggested being the only other species where dominant individuals conceal sex regularly. We examined whether birds indeed conceal sex and tested different hypotheses postulating that sex concealment functions to avoid predators, signal dominance status, or to avoid social interference. The results showed that the birds concealed sex in all observed cases of copulation, did not prefer to copulate under shelters and concealed mating solicitations from adult conspecifics. In addition, subordinates did not attack dominants who courted the respective female. Hence, none of the tested hypotheses explains these results satisfactorily. We postulate that dominant Arabian babblers conceal sex to maintain cooperation with those helpers they prevent from mating. Empirical desiderata for testing this 'Cooperation-Maintenance' hypothesis are discussed.

1. Introduction

The diversity of cultures (Davenport, 1987) and mating systems (e.g., monogamy, polyandry; Schmitt, 2005) that have evolved in the human species (*Homo sapiens*) is manifold. Striking uniformity, however, exists in humans' preference for concealing sexual interactions from the view of other conspecifics (Ford & Beach, 1951). For example, across cultures sexual activity occurs inside private dwellings (Ford & Beach, 1951), away from the residential village (e.g., Yanomamö in Venezuela; Chagnon, 1997), or in the darkness of the night (e.g., Zapotec in Mexico; Taylor, 1979). Even married couples take active precautions to keep their sexual encounters private. Malekula couples from Melanesia, for instance, were reported to return home from the mating place in different directions (Deacon & Wedgwood, 1934) and Mehinaku pairs in Brazil have intercourse in agreed secret locations (Gregor, 1985). If privacy cannot be achieved, couples often suppress their sexual activity (e.g., the agricultural culture in Melanesia; Davenport, 1987). The preference to conceal sex has thus long been considered as a human universal (Friedl, 1994; MacCurdy, 1930; Symons, 1979; van Schaik, 2016), and even as a uniquely human trait (Diamond, 1992; Ford & Beach, 1951). Furthermore, it has been speculated that

concealed sex significantly influenced the evolution of humans' emotions (e.g., shame; MacCurdy, 1930) and sophisticated cognitive skills (e.g., modelling of social relations; Friedl, 1994).

In spite of almost a century of interest in humans' preference to conceal sex, the writing about the topic is anecdotic and scientific investigations are non-existent (Friedl, 1994; MacCurdy, 1930; van Schaik, 2016). Thus, the function fulfilled by this behaviour and the selective pressures driving its evolution remain unclear (Friedl, 1994; van Schaik, 2016). One reason for human couples to conceal sex is the preservation of social norms. For instance, individuals living in serial monogamous societies but engaging in extramarital sex conceal their sexual affairs to avoid being interrupted and to escape social punishment (Howie & Pomiankowski, 2016; Schröder, 1993). However, the question of why humans conceal sexual interactions even when they are in socially accepted relationships (e.g., formalized partnerships, marriages) still remains a puzzle. Some scholars suggested that concealed sex in humans is a strategy to avoid overt reproductive competition (Friedl, 1994; MacCurdy, 1930; Suggs, 1966; Symons, 1979; van Schaik, 2016). This hypothesis however fails to explain why concealed sex evolved to be the norm in humans, but does not play a significant role in other animal species especially in our closest living relatives, the

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great apes (Ben Mocha and Pika, in preparation).

In the absence of systematic, quantitative studies and the ethical limitations of behavioural experiments on concealed sex in humans (Diamond, 1992), a cross-species comparative approach may shed important light on the selective pressures driving the evolution of this preference (van Schaik, 2016). In nonhuman species, elusive mating behaviour has been reported in a wide range of taxa, such as for instance carnivores (e.g., *Helogale parvula*: Creel, Creel, Wildt, & Monfort, 1992; *Crocota crocota*: Kruuk, 1972), passerines (e.g., *Prunella collaris*: Davies, Hartley, Hatchwell, & Langmore, 1996; *Chiroxiphia linearis*: McDonald & Potts, 1994), primates (e.g., *Ateles belzebuth chamek*: Gibson, 2010; *Theropithecus gelada*: le Roux, Snyder-Mackler, Roberts, Beehner, & Bergman, 2013), and ungulates (*Ovis canadensis*: Hogg, 1984). In these species, however, the use of concealed sex is mainly restricted to subordinate individuals and is only rarely used by dominants (Ben Mocha and Pika, in preparation). In addition, in these species sexual interactions are often disrupted by conspecifics (Ben Mocha and Pika, in preparation). Thus, similarly to socially unaccepted couples in humans, subordinate animals may conceal sex to avoid harassment by conspecifics (Howie & Pomiankowski, 2016; Niemeyer & Anderson, 1983). Yet, why would dominant animals – defined here as individuals that are able to use their dominance to suppress interference – need to conceal sexual activity? Here, we argue that this question for nonhuman species is equivalent to the anthropological question about the motives of socially accepted human couples to conceal sex.

Regular concealed sex within dyads of dominant individuals has so far only been suggested by “preliminary observations” in a single non-human animal species - the cooperatively breeding Arabian babbler (*Turdoides squamiceps*) (Zahavi, 1988, 1990). Arabian babblers are passerine birds that live all year long in stable social groups of two to 20 individuals (Zahavi, 1989). Groups vary in their composition and show all combinations of age, sex and kin relations (Zahavi, 1989). The dominant pair produces 95% of the offspring (Lundy, Parker, & Zahavi, 1998), but relies strongly on systematic alloparental care of other group members (e.g., by feeding the nestlings; Ostreiher, 1997; Ridley, 2007).

Arabian babblers are distantly related to humans in phylogenetic terms. Yet, similar behaviours may have evolved due to similar selection pressures (Emery & Clayton, 2004). Consequently (and similar to other scientific fields trying to understand human evolution, e.g., language evolution; Hauser, Chomsky, & Fitch, 2002), investigations of behavioral phenomena due to convergent evolution are powerful tools to understand the factors driving the evolution of the behaviours in question. Thus, to shed light on the selective pressures that may have driven the evolution of concealed sex, we re-visited Zahavi's claim that dominant Arabian babblers regularly conceal sex from conspecifics (Zahavi, 1988). To achieve this goal, we studied the behaviour of a wild population of individually marked Arabian babblers living in the Shezaf Nature Reserve in Israel.

We addressed the following two questions: First, do Arabian babblers regularly conceal sex from conspecifics regardless of their dominance rank? To answer this question, we followed the approach by Overduin-de Vries, Spruijt, Vries, and Sterck (2015) and paid special attention to two behavioural strategies implicated with tactical deception: “using peripheral locations” (i.e., the pair increases its distance from bystanders to > 100 m) and “hiding behind opaque objects” (i.e., both individuals position themselves on one side of an opaque object, while the audience is on the opposite side). If Arabian babblers conceal sex, we predicted that copulation attempts (defined here as “the female bends over by lowering her head and raising her tail, while the male mounts her”) would be performed at times and/or in locations hidden from the view of other group members. Second, if Arabian babblers engage in concealed sex, what is the function of this behaviour? Motives for concealment of sex have not been studied intensively (Ben Mocha and Pika, in preparation). We therefore investigated the function fulfilled by this behaviour by testing three different hypotheses: First, the *Predation*

Table 1

Hypotheses previously suggested explaining concealed mating behaviour in different species and their predictions.

Hypothesis	Suggested for (examples)	Function of concealed sex	Predictions
<i>Predation Hypothesis</i>	Humans (<i>Homo sapiens</i> ; MacCurdy, 1930); Richardson's ground squirrels (<i>Urocitellus richardsoni</i> ; Davis, 1982)	To avoid predation while attention is focused on copulation.	(a) Solicitation of copulations would be independent of conspecifics presence; (b) Copulations would occur in sheltered locations.
<i>Dominance Signalling Hypothesis</i>	Arabian babblers (<i>Turdoides squamiceps</i> ; Zahavi & Zahavi, 1997)	To signal dominance over other males by deterring them from interrupting the privacy of copulation.	Dominants would solicit copulations in the presence of subordinates but not vice versa.
<i>Social Interference Hypothesis</i>	Humans (Suggs, 1966); Dunnocks (<i>Prunella modularis</i> ; Davies et al., 1996)	To avoid physical interference by conspecifics.	(a) Conspecifics would respond with aggression to others' mating; (b) Solicitation of copulations would not be prolonged.

Hypothesis, which was proposed to explain the rarity of observed copulations in some species (Davis, 1982). Second, the *Dominance Signalling Hypothesis* that explicitly aimed to explain concealed sex in the Arabian babbler (Zahavi, 1988). Third, the *Social Interference Hypothesis*, which was postulated to explain concealed sex in species characterized by frequent interruptions of sexual interactions by conspecifics (Davies et al., 1996; see Table 1 for a summary of hypotheses and their predictions).

The “*Predation Hypothesis*”, originally proposed to explain concealed sex in humans (Eibl-Eibesfeldt, 1989; MacCurdy, 1930), was subsequently applied to illuminate underground mating in several ground squirrel species (e.g., *Urocitellus richardsoni*, Davis, 1982; Michener, 2001). It postulates that interactants - with their attention being focused on the copulation itself - would preferentially mate in protected locations to avoid predation. If this hypothesis also applies to Arabian babblers, we predicted to find that solicitations of copulation would occur independently of conspecifics' presence. In addition, to ensure safety partners would copulate within shelters (that protect them from predator attacks) rather than in open arrays.

The “*Dominance Signalling Hypothesis*” (Zahavi, 1988, 1990; Zahavi & Zahavi, 1997) postulates that Arabian babbler males conceal sex to signal their degree of dominance over other males in the group by deterring them from interrupting the privacy of copulations. The female, in turn, uses this information to “share her favors according to the relative importance of her partners” within the group (Zahavi & Zahavi, 1997, p. 146). If Arabian babblers indeed conceal sex to signal their dominance, we predicted that dominant males would solicit copulations in the presence of subordinates. This would allow the females to reliably distinguish dominants, which initiate “private” copulation as a signal, from subordinates, which conceal solicitation of copulations to avoid harassment.

The “*Social Interference Hypothesis*” suggests that concealed sex occurs in species where group members aggressively interfere with conspecifics' mating attempts. Here, individuals actively seize opportunities when alone with their mating partners to solicit copulation. This hypothesis has predominantly been applied to explain concealed sex in a variety of species such as, for instance, humans (Suggs, 1966), Rocky mountain bighorn sheep (*Ovis canadensis*; Hogg, 1988), and Dunnocks (*Prunella modularis*; Davies et al., 1996). If concealed sex in the Arabian babblers is used to avoid physical interference of group members, we predicted that sexual interactions would be accompanied by aggressive interventions of observers. In addition, to promote the completion of copulation, individuals would avoid prolonged communicative

signalling to initiate copulations.

To test these hypotheses, we focused on episodes of “*OBJECT PRESENTATION*”¹, a distinct gestural communicative behaviour often used by individuals of this bird species to solicit mating. It is defined as “*an individual picking up an object with its beak, holding it in front of an opposite-sex conspecific and waiting for its response*”. We investigated (i) whether solicitations of copulations were concealed from conspecifics, (ii) whether the chosen mating location was protected from predators, (iii) whether dominant and subordinate individuals differed in their preference to conceal *OBJECT PRESENTATIONS*, (iv) the behavioural responses involved when a third party approaching the dyad during *OBJECT PRESENTATIONS* and/or copulation attempts, and (v) whether copulation attempts were initiated by *OBJECT PRESENTATIONS*.

2. Materials and methods

2.1. Study site and population

Data were collected within and at the fringe of the ‘Shezaf Nature Reserve’ (30.718N/35.266E) in Israel. A long-term study on the reserve’s Arabian babbler population has been carried out since 1971, with birds being well habituated to human observers. Each bird was banded with a unique combination of four coloured rings, and the adult males and females could be reliably distinguished by the colour of their iris (Zahavi, 1989). The life history of all individuals, including their dominance ranks, has been recorded continuously (Ben Mocha, 2014; Zahavi, 1989). All individuals observed were sexually mature (older than one year of age) and all social groups consisted of a breeding pair and one to nine adult helpers (mean \pm SD of group size: 6 ± 3).

2.2. Behavioural observations

Data were collected during three breeding seasons (January–June 2010, August 2011–July 2012 and February–June 2014). Daily observations were carried out during the most active time of the birds (Dattner, 2005), i.e., in the first four hours after dawn when the group had left its roosting tree and during the two hours before dusk when the group returned to its roosting tree. The data collected in 2010 and 2012 are part of a larger study on social behaviour of Arabian babblers (Ben Mocha, 2014). They include opportunistic observations of *OBJECT PRESENTATIONS* ($n = 8$) and copulation attempts ($n = 22$). Data were documented via the study logbook and a series of still photos taken with a digital camera (Nikon D90; 4.5 frames per second) equipped with a telephoto lens (Nikkor 18–200 mm VR II). The data collection carried out in 2014 focused systematically on *OBJECT PRESENTATIONS* ($n = 56$) and copulation attempts ($n = 34$). It resulted in a total of 144.7 h of focal observations during 86 observation sessions. Behaviours were recorded from a distance of 2–20 m using a digital High-Definition camera (Canon LEGRIA HFM 41) with an internal microphone. This method enabled the collection of high-quality footage combined with simultaneous observer comments of the respective behaviour (behaviour sampling rule, Martin & Bateson 1994). After Arabian babblers have constructed their nest, an egg is laid each morning over three to six consecutive days and most copulations occur during this time (Perel, 1996; Zahavi, 1989). Hence, to document *OBJECT PRESENTATIONS* and copulation attempts, we followed the dominant females of the study groups during this egg-laying period. A Smartphone (Samsung Galaxy 2) with CyberTracker (CyberTracker) software was used to record the following data for each episode: (i) ID’s of interactants’, (ii) time of occurrence, (iii) whether the behaviours (*OBJECT PRESENTATION*/copulation attempt) were performed > 100 m away from the rest of the group or not, (iv) who moved away from whom before the copulation attempt (the group or the dyad), (v)

whether the behaviours took place within or behind thick vegetation that blocked visual contact between the dyad and the group, (vi) whether signallers of *OBJECT PRESENTATION* had actively guided recipients (distance of > 5 m) to reposition themselves behind vegetation cover, (vii) the behavioural responses that occurred within 30 min after a third party approached the dyad during *OBJECT PRESENTATION* or a copulation attempt, (viii) whether or not a copulation was preceded by an *OBJECT PRESENTATION*, (ix) whether the copulation occurred within vegetation cover (e.g., acacia trees, *Acacia*; see videos S1 and S2) that could be regarded as a shelter from mammalian and aerial predators, and (x) whether such a cover was available within 10 m of the actual location of the copulation.

2.3. Statistical analyses

Statistical analyses were conducted using the program R, version 3.3.3 (R Core Team, 2017) with the package lme4 (version 1.1–13; Bates, Maechler, Bolker, & Walker, 2015). All tests were two-tailed and the significance level was set to $\alpha = 0.05$. Due to the elusive nature of the species’ mating behaviour, data for some criteria were not always available. In these cases, we report a different sample size. Generalized Linear Mixed Models (GLMM) (Baayen, 2008) were used to account for pseudoreplication (Waller, Warmelink, Liebal, Micheletta, & Slocombe, 2013). All models had a binomial error structure, logit link function (McCullagh & Nelder, 1989) and included the signaller, recipient, dyad and social group identities as random intercept effects. The significance of each full model as compared to its corresponding null model (containing only the intercept and random effects; Forstmeier & Schielzeth, 2011) was examined using a likelihood ratio test (R function “anova” with argument test “Chisq”; Barr, Levy, Scheepers, & Tily, 2013; Dobson & Barnett, 2008). We assessed the stability of each model by excluding each level of the random effects one at a time from the dataset and comparing model estimates derived from these data with the ones derived from the full data set. To keep type I error rate at the nominal level of 5% we checked which random slopes (Barr et al., 2013; Schielzeth & Forstmeier, 2009) were identifiable, i.e., sufficiently varied within the levels of the random effects included in the respective model. This did not reveal identifiable random slopes to exist.

2.3.1. Do Arabian babblers conceal copulation attempts and *OBJECT PRESENTATIONS* from conspecifics?

We examined whether *OBJECT PRESENTATIONS* and copulation attempts were more likely than expected to occur when the group is away (> 100 m). To do this, we analysed data for *OBJECT PRESENTATIONS* and copulation attempts in two separate GLMMs. The distance between the group and the dyad (> 100 m / < 100 m) was set as the response variable. The dominance rank of the signaller (dominant for alpha males and females/subordinate for other group members) was set as a fixed effect. We then bootstrapped ($n = 1000$) 95% confidence limits of the estimated probabilities of these behaviours to occur away from the group and compared them to the baseline proportion of time individuals were observed to be away from their group. To this end, during the breeding season of 2012 we continuously monitored whether there was at least one group member away (> 100 m) from its group ($n = 4$ social groups, 288 observation hours). Note that this is a conservative approach as most of the copulations documented in our study took place between the breeding pair, while here we estimated the percentage of time any other group member was absent. As previous studies also confirmed that Arabian babblers spend the majority of the day in close proximity to their group members (Dattner, 2005; Zahavi, 1988), we generalized this result from 2012 to the entire research period. Sample size for the copulation attempts model was 51 copulation attempts involving 16 signallers and 15 recipients forming 18 dyads from 11 groups. Sample size for the *OBJECT PRESENTATION* model was 63 *OBJECT PRESENTATIONS* involving 14 signallers and 14 recipients forming 16 dyads from 11 groups.

¹ From here on, the gesture object presentation is depicted in small capitals.

In addition, we examined whether Arabian babblers use peripheral locations and hiding behind an opaque object as alternative strategies to conceal OBJECT PRESENTATIONS. To this end, we set a GLMM with the following response variable: an opaque object was located between the dyad and the group during an OBJECT PRESENTATION (no/yes). The signaller's dominance rank and whether the group was > 100 m away (yes/no) were set as fixed effects. Sample size for this model was 59 episodes that involved 13 signallers, 13 recipients forming 15 different dyads from 10 social groups.

2.3.2. Do copulations occur in shelters protecting from predators?

To examine whether Arabian babblers concealed sex in order to ensure safety from predation, we tested whether copulations were more likely to occur within vegetation cover when possible. We therefore confirmed that potential shelters were available within 10 m of all actual copulation sites. The GLMM included the protection of the copulation site (sheltered/not sheltered) as the response variable. We tested the probability of a copulation attempt to occur within a shelter by testing the intercept of the model after removing dominance rank (which appeared non-significant) by means of Wald's z-approximation (Field, 2005). Sample size was 56 copulation attempts that involved 16 signallers and 15 recipients forming 18 dyads from 11 social groups.

2.3.3. Do conspecifics respond conspicuously or aggressively to others' mating behaviour?

To investigate whether Arabian babblers conceal sex to avoid physical interference, we documented any instance of these behaviours within 30 min of the appearance of a group member during others' performing an OBJECT PRESENTATION or a copulation attempt.

3. Results

3.1. Do Arabian babblers conceal sex from conspecifics?

A total of 56 copulation attempts in 18 different dyads was documented. The copulations involved 13 alpha females, seven alpha males (n = 41), and eight subordinate males (n = 15).

All documented episodes (100%) were concealed from all other group members by at least one of the investigated strategies for tactical deception (see Fig. 1a): 73% of all observed copulation attempts occurred when the dyad was > 100 m away from its social group (i.e., concealment by using peripheral locations; n = 51 episodes). 87% of copulation attempts occurred behind or within vegetation (e.g., salt tree, *Nitraria retusa*) that prevented visual contact between the mating pair and its group (i.e., concealment by hiding behind an opaque object; n = 55 episodes).

Copulating dyads were not isolated from their groups because the latter simply moved further while the dyad engaged in prolonged courting. Rather in 84% of copulation attempts it was the dyad that had actively moved to conceal itself from other group members' view (n = 43): In six episodes, the dyad actively left its social group (> 100 m); in 17 episodes the signaller of OBJECT PRESENTATION lead the recipient a short distance (5–50 m) to copulate behind vegetation cover; and in 13 episodes the dyad flew > 100 m away from the group and later moved locally to position itself behind vegetation cover. In only seven episodes, the dyad had stayed behind while the group had moved > 100 m away from it, and it did not further reposition itself behind cover. Four out of these seven episodes were “opportunistic” copulation attempts of subordinate males with the dominant female (see result 3.4.2).

The probability of copulation attempts to occur away from the group was larger than expected given the proportion of time individuals were observed to stay away from their group during the breeding season (mean ± SD: 11 ± 8%, range among groups: 3–22%; Fig. 2).

3.2. The predation hypothesis

3.2.1. Does solicitation of copulations occur independent of conspecifics presence?

We recorded a total of 64 OBJECT PRESENTATIONS performed by six alpha males (n = 51), two alpha females (n = 3), and six subordinate males (n = 10).

One hundred percent of OBJECT PRESENTATIONS were concealed from all adult members of the group by using at least one of the strategies qualifying as tactical deception (Fig. 1b): Sixty-seven percent of all OBJECT PRESENTATIONS were produced when the group was away (> 100 m) from the signaller (n = 64). Sixty-three percent of OBJECT PRESENTATIONS were performed after the signaller actively positioned itself behind an opaque object so that it was visible to the recipient only (n = 60). For instance, when the recipient was on top of a bush and the group foraged on one side of the bush, the signaller moved to the opposite side and signalled from there. We observed only two OBJECT PRESENTATIONS occurring in the presence of a group member. Both instances, however, involved a dependent fledgling (< 3 months old) as the audience and failed to elicit a response.

Similarly to copulation attempts, the proportion of OBJECT PRESENTATIONS produced away from the group was larger than expected given the proportion of time individuals were observed away from their group (11%; Fig. 2). Furthermore, signallers used peripheral locations and hiding behind an opaque object as alternative strategies: OBJECT PRESENTATIONS tended to occur with a higher frequency from behind an opaque object when the group was nearby (< 100 m) than when the group was > 100 m away (GLMM: $\chi^2 < 5.87$, df = 1, P = 0.015 Table 2).

3.2.2. Do copulations occur in shelters protecting from predators?

Travelling to shelters from predators (e.g., umbrella thorn acacia: *Acacia tortilis*) imposed no time or energetic costs as potential shelters were available within < 10 m of all 56 locations where copulation attempts occurred. Yet, only 29 copulation attempts took place within or under vegetation and there was no significant preference to copulate within shelters (test of the intercept: 0.08 ± 0.3; P = 0.8, see videos S1 and S2).

3.3. The dominance signalling hypothesis

3.3.1. Do dominant individuals solicit copulations in the presence of subordinates?

As presented above, dominant (n = 54) and subordinate individuals (n = 10) concealed 100% of their OBJECT PRESENTATIONS from adult group members. One of the two OBJECT PRESENTATIONS that occurred in the view of dependent fledglings was performed by a dominant male and the other by a subordinate male.

3.4. The social interference hypothesis

3.4.1. Do conspecifics respond aggressively to others' mating behaviour?

We observed nine OBJECT PRESENTATIONS and six copulation attempts in which other group members appeared during sexual interaction. An additional case involved the beta male observing the dominant pair copulating through a bush (see video S2). Out of these 16 episodes, nine involved subordinates appearing during an interaction between the alpha pair. Seven episodes involved the appearance of a higher-ranking male during an interaction between a lower-ranking male and the alpha female. In all 15 episodes in which the mating dyad noticed the third party, the dyad immediately dropped the object used for presentation and terminated its sexual behaviour. In only one episode, a beta male chased away the gamma male that attempted to copulate with the alpha female. Beside this exception, we did not observe any cases of physical aggression following these episodes. Dominance displays by alpha males were unidirectional towards subordinates that

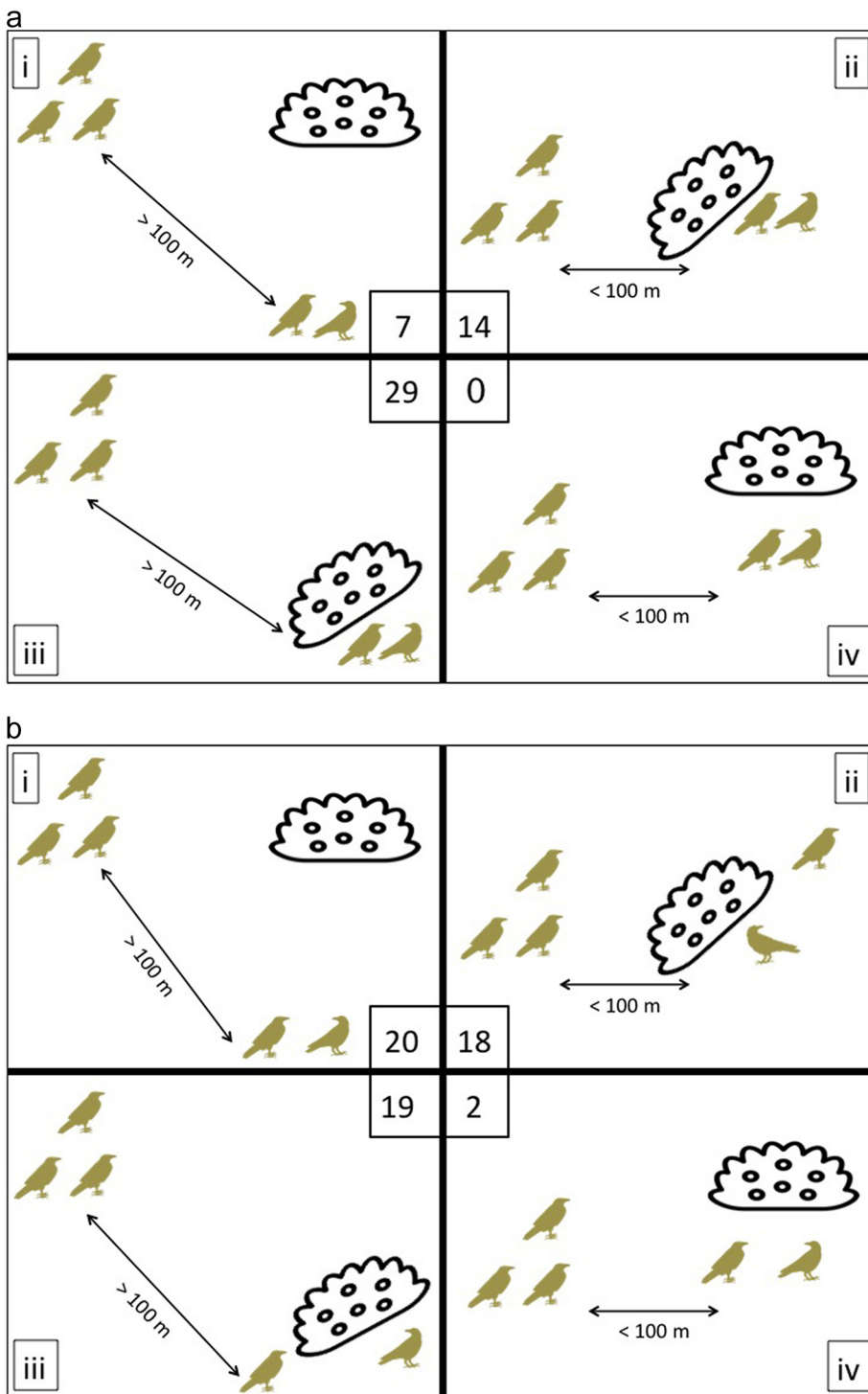


Fig. 1. Behavioural tactics used by Arabian babblers to conceal (a) copulation attempts and (b) solicitation of copulations. Depicted are the total numbers of observed episodes (in the centre) in which (a) copulation attempts and (b) solicitations of copulations occurred when the dyad was (i) > 100 m away from the group, but not behind an opaque object, (ii) < 100 m away from the group, but behind an opaque object, (iii) > 100 m away from the group and the dyad/signaller was behind an opaque object, and (iv) < 100 m away from the group and not behind an opaque object. Only episodes for which the distance and the location of the group were known are presented.

interrupted the privacy of OBJECT PRESENTATIONS and towards subordinates who courted the dominant female (see video S3 and Table S1 for description of all interactions).

3.4.2. Do individuals solicit copulations without prolonged communication?

All copulation attempts by alpha individuals were initiated by OBJECT PRESENTATIONS (n = 39). However, about one third of subordinate males' copulation attempts were not initiated by OBJECT PRESENTATIONS (5 out of 14 episodes). All copulation attempts that were not solicited by OBJECT PRESENTATIONS had common characteristics: (i) They occurred after the alpha male suddenly left the proximity of the dyad (e.g., for chasing intruders); (ii) the dyad

copulated immediately where it had been “left alone” by the dominant; and (iii) the female fully cooperated with the male by bending over for mating posture immediately. We did not identify prominent communicative signals that preceded these copulation attempts, but they may have been initiated by the female who first bended-over for copulation posture (see video S3).

4. Discussion

The present study aimed to provide insight into the selective pressures driving the evolution of concealed sex. We observed the sexual behaviour of Arabian babblers, which have been suggested as the only

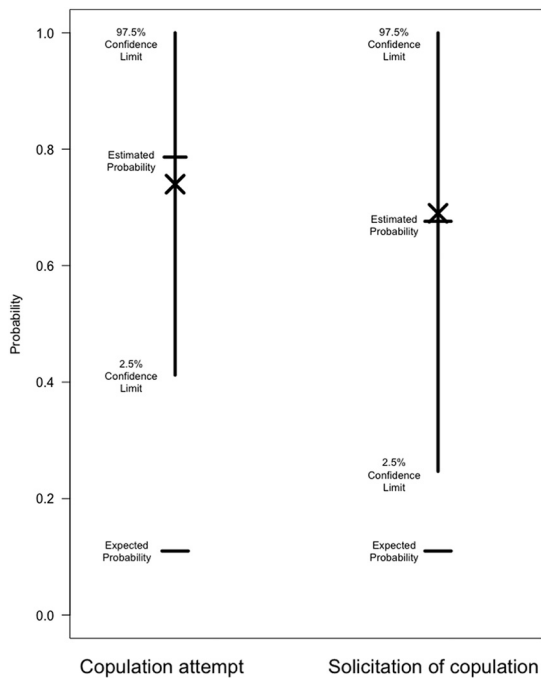


Fig. 2. Observed, expected and estimated probabilities of copulation attempts and solicitations of copulations to occur when the group was away from the dyad. X denotes the *Observed Probabilities* of copulation attempts and solicitations of copulations that occurred when the group was away (> 100 m) from the dyad. The *Expected Probabilities* of copulation attempts and solicitations of copulations to occur when the group was away are based on the mean proportion of time when at least one individual was observed away from its group during the breeding season (11%). The *Estimated Probabilities* and *95% Confidence Limits* of copulation attempts and solicitations of copulations to occur when the group was away are based on a bootstrap analysis of GLMMs estimates.

Table 2

Factors influencing the probability of OBJECT PRESENTATIONS to occur behind opaque objects.

Term	Estimate	SE	χ^2	df	p
Intercept	2.210	0.971			
Dominance rank of signaller (subordinate)	-0.472	1.260	0.136	1	0.712
Group > 100 m away from signaller (yes)	-2.122	0.958	5.870	1	0.015

Generalized Linear Mixed Model based on 59 OBJECT PRESENTATIONS.

nonhuman animal species to regularly engage in concealed sex between dominant individuals (Zahavi, 1988). We addressed two research questions: First, do Arabian babblers regularly conceal sex from conspecifics regardless of their dominance rank? Second, if they do, what is the function of concealed sex in this species?

Overall, we found that (i) dominant and subordinate group members solicited copulations and attempted to copulate exclusively at times and/or in locations where they could not be seen by other adult members of their group; (ii) dyads did not show a preference to copulate within protected shelters; (iii) no physical aggression was shown when subordinates appeared during sexual interactions of the dominant dyad; (iv) higher ranking males responded with aggression and dominance displays to terminate lower-ranking males' mating behaviour; and (v) subordinates, but not dominants, regularly engaged in opportunistic copulations that were not solicited by OBJECT PRESENTATIONS.

The finding that all copulation attempts were concealed from adult group members provides the first systematic support for Zahavi's

observations (Zahavi, 1988). These findings further show that Arabian babblers use two strategies in line with tactical deception to conceal their sexual activity: Using peripheral locations and hiding behind opaque objects (Overduin-de Vries et al., 2015). The cognitive abilities that underlie these behaviours should be further studied (e.g., whether Arabian babblers are able to discriminate their own visual perspective from that of the audience).

Concerning the function of concealed sex in Arabian babblers, we tested predictions resulting from three alternative hypotheses. Since solicitations for copulations did not occur independently of conspecific presence (Figs. 1b and 2) and copulations did not tend to occur within shelters from predators, we could rule out the *Predation Hypothesis*.

The results also did not support predictions for the *Dominance Signalling Hypothesis* - i.e., that dominant males solicit copulations in the presence of others to signal their dominance over subordinates – since dominants concealed all of their OBJECT PRESENTATIONS from adult group members.

We found that aggressive responses and dominance displays were only produced by dominants towards lower ranking individuals who engaged in sexual behaviour. In accordance with previous studies on our model species (Perel, 1996; Zahavi, 1988, 1990), subordinates were never observed to physically interrupt dominants' mating behaviours. Furthermore, only subordinate males were involved in opportunistic copulations that were not preceded by prolonged communication. These results support the predictions formulated for the *Social Interference Hypothesis*. However, they only satisfactorily explain the use of concealed sex by subordinate Arabian babblers.

We therefore argue that subordinate and dominant Arabian babblers may conceal sex for different purposes. Similarly to subordinate individuals in other nonhuman species (Ben Mocha and Pika, in preparation), subordinate Arabian babblers conceal sex to avoid physical interference by more dominant individuals. However, the findings that dominants (i) actively concealed mating behaviour from subordinate helpers, and (ii) terminated courtships when being observed by them, although not been interrupted physically, are in sharp contrast to the predictions made by all hypotheses tested. Hence, as a posteriori explanation, we postulate that concealed sex by dominant Arabian babblers fulfils a different and so far unrecognized function. As a proximate mechanism, concealed sex is used to prevent further social tension between group members. At the ultimate level, it functions to maintain cooperation and allopaternal care within the social group. While subordinate Arabian babblers provide crucial allopaternal care (Ridley, 2007), they are prohibited from mating (Perel, 1996), especially during the alpha female's fertile period (Lundy et al., 1998). Concealing triggers for social conflicts thus might reduce the chances of helpers dispersing or fighting with the alpha individuals over their breeder position – two results with a significant negative effect on the alpha pair's reproductive fitness (Keynan & Ridley, 2016). Indeed, the breeding season of Arabian babblers is characterized by increased social tension between the dominant pair and their helpers (Dattner, 2005). Therefore, although the species' social system includes intense cooperative behaviours, it is also characterized by intense competitive interactions (Zahavi, 1990; Zahavi & Zahavi, 1997). Individuals thus need to constantly balance and negotiate their social relationships, resulting in multifaceted nonaggressive strategies to avoid overt social tension and to maintain cooperation (e.g., allopreening: Dattner, 2005; allofeeding: Kalishov, Zahavi, & Zahavi, 2005).

Key features of concealed sex have so far not been quantified in many species. We thus hope that this first report on regularly concealed sex by dominants in a nonhuman animal species will encourage more studies in other carefully selected model species. In particular, our study may be useful in shedding light on the evolutionary puzzle of concealed sex in humans. We propose that although concealed sex may fulfil different functions in different species (e.g., to avoid predation or social interruption), the phenomenon may also have evolved independently in distantly related species due to similar selection

pressures. Specifically, we propose that concealed sex by dominant nonhuman animals and humans living in socially accepted relationships evolved as a function of two conflicting motives: (1) Some group members' mating are suppressed - at least with some specific individuals (for examples in humans see [Daly, Wilson, & Weghorst, 1982](#); for examples in nonhuman species see [Young, Spong, & Clutton-Brock, 2007](#)); and (2) one's reproductive fitness depends on collaboration with those individuals whose mating behaviour is suppressed. This conflict characterizes the social system of Arabian babblers ([Zahavi, 1989](#)) but can also be found in many human societies. First, virtually all human societies are built upon social norms that allow sexual relationships among adults with specific partners only (e.g., through marriage [Ford & Beach, 1951](#)). Thus although all members of a given society may have a sexual partner, sexual relationships with other community members are suppressed, with those breaking this social norm often receiving severe punishment ([Daly et al., 1982](#)). Second, at the same time, humans' fitness crucially depends on alloparental care provided by group members, which are often non kin at their reproductive age ([Hill & Hurtado, 2009](#); [Hrdy, 2007](#); [Quinlan & Quinlan, 2008](#)). We therefore suggest that concealed sex functions to maintain cooperation within societies of highly cooperative humans that, at the same time, restrict sex between specific partners only.

As for any post-hoc hypothesis postulated to explain the evolutionary origins of behaviour, our arguments are only as good as the amount of available comparative evidence (i.e., the number of species tested). We thus conclude with a brief set of empirical desiderata and hope that it will instigate more studies of this fascinating subject (and potentially falsify our claims). Our proposal is that concealed sex evolved to maintain cooperation when fitness strongly depends on cooperation with group members who are prevented from mating. The main prediction that follows is that dominant individuals will conceal sex in social systems that fulfil at least two conditions: First, mating is suppressed at least to some extent (e.g., with specific group members, during the fertility period of the female); and second, fitness dependency on cooperation. A third condition may be the presence of potential mates other than close kin in the social group. A next possible step to test this prediction will be to explore concealed sex in distantly related species that breed cooperatively and show monopolization of mating (e.g., Florida scrub jays, *Aphelocoma coerulescens*; [Mumme, Bowman, Pruett, & Fitzpatrick, 2015](#); pygmy marmosets, *Cebuella pygmaea*; [Soini, 1987, 1988](#)). In addition, since human societies show considerable variability in their degree of cooperation and sexual liberty in particular ([Davenport, 1987](#)), future studies should explore the cultural variation in the degree of sex concealment. Specifically, we predict that when dependency on cooperation is weaker or sexual liberty is higher, sexual privacy would be milder and vice versa (for potential examples see [Crocker, 1990](#); [Rival, 2016](#)).

5. Conclusions

Here, we provide the first systematic evidence that dominant Arabian babblers regularly engage in concealed sex - a behaviour that has previously been suggested as a "human universal" ([Friedl, 1994](#)) and uniquely human ([Diamond, 1992](#); [Ford & Beach, 1951](#)). With regards to the function of this behaviour, we show that dominant Arabian babblers do not conceal sex to signal their dominance, to avoid predation, or to avoid physical interruption by subordinate group members. We suggest that concealed sex by humans and distantly related species such as the Arabian babblers evolved through convergent evolution triggered by the need to maintain intensive cooperation whilst suppressing collaborators' mating relationship within the social group. This called "Cooperation-Maintenance" hypothesis is the first to articulate testable predictions for the evolution of concealed sex in humans: Regularly concealed sex will occur in those animal species showing comparable level of mating monopolization and heavy reliance on cooperative support.

- Icons used in [Fig. 1](#) were made by Freepik from www.flaticon.com

Data availability

The datasets generated during the current study are available from the corresponding author on reasonable request.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.evolhumbehav.2018.05.009>.

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