



Norwegian University of
Science and Technology

Safe, selfish state-independent mobbing behaviour in the cooperatively breeding apostlebird (*Struthidea cinerea*)

Erlend Berne

Biology

Submission date: May 2011

Supervisor: Jonathan Wright, IBI

CONTENTS

Acknowledgements	2
Abstract	2
Introduction	3
Mobbing behaviour in birds	3
Mobbing in cooperative breeders	7
State-dependent mobbing behaviour	8
Aims of the study	11
Methods	12
Study Species	12
Study Site	12
Experimental method	12
Schedule	15
Video analysis	16
Genetic Analysis	17
Data Analysis	17
Results	19
Distance as measure of mobbing	19
Within-individual differences in distance	20
Assessing state-dependence	23
Between-subject effects	25
Group level effects	27
Discussion	29
References	33

ACKNOWLEDGEMENTS

This thesis was completed at the Norwegian University of Science and Technology (NTNU), with the supervision of Professor Jonathan Wright. Fieldwork was carried out at Fowlers Gap, NSW Australia, with all appropriate licenses and permits from ABBS (Australian Bird and Bat Banding Scheme) and Macquarie University Ethics Committee (via Dr. Simon Griffith). My project would not have been possible without the following people, whom I wish to give my deepest thanks:

Claire F.R. Wordley, Claudia A. F. Wascher, and Erin S. Morrison for their tireless persistence and invaluable help in the field, Jonathan Wright for his great patience and crucial feedback when writing up this thesis, Simon Griffith and Miya Warrington for the genetic data, and Garry and Vicki Dowling for their generous hospitality at Fowlers Gap. Additional thanks go to my family, friends and beloved for their moral support.

ABSTRACT

In the last few decades stochastic dynamic modelling (SDM) has been used to explore adaptive state-dependent strategies in a whole host of different theoretical problems in behavioural ecology, with considerable success. It has allowed us to better understand cooperative behaviours such as sentinel behaviour, and it might allow us to more fully understand other cooperative behaviours with alternative dynamics. In a recently developed SDM, anti-predator behaviour was examined and a counter-intuitive prediction has emerged: that mobbing effort should be completely independent of state. In this study we test this interesting prediction, using the cooperatively breeding apostlebird (*Struthidea cinerea*) as our study species. From October 15th to November 21st in 2009, 6 groups of varying sizes were put through a set of trials, where we used a rubber snake model to elicit mobbing behaviour in experimental trials. A similarly sized stick was used during control trials, wherein birds tended to forage. Behaviour, placement and vocalisation data on an individual basis were gathered in multiple scan samplings per trial in both kinds of treatment. This highly accurate data was then compared with within-individual differences in body mass (state). Several other variables were also considered: sex, age, breeding status, relatedness and mean body mass. Results show that while foraging behaviour was highly state-dependent during controls, no such effect was found in the mobbing effort of the same individuals during experiments. Mobbing effort also did not vary with any of the mentioned phenotypically fixed variables. Our study therefore offers the first empirical evidence of state-independent mobbing.

INTRODUCTION

When animals are confronted with a predator, natural selection might be expected to favour behaviour that minimizes individual predation risk, such as evasion of detection and capture (Sih 1987; Lima & Dill 1990; Endler 1991). However, a surprisingly large collection of data shows that some vertebrate prey will actually repeatedly approach, closely observe and even physically attack predators. This has been observed in fish (Dominey 1983; Pitcher et al. 1986; Helfman 1989; Foster & Polch 1990; Dugatkin & Godin 1992), mammals (Walther 1969; Kruuk 1972; Owings & Coss 1977; Loughry 1987; Cheney & Seyfarth 1990), and birds (Altmann 1956; Kruuk 1976; Curio 1978; Shields 1984). The ways in which prey confront predators in this manner is very varied, and when studying its adaptive importance it is important to be aware of the different ways in which such anti-predator monitoring, ‘mobbing’ or harassment behaviour manifests itself. For example, a common mobbing behaviour might be to produce loud vocalisations (Owings & Owings 1979; Brown 1985; Klump & Shalter 1984; Curio & Regelman 1985; Cheney & Seyfarth 1990). Other mobbing behaviours include distraction or threat displays during the approach towards the predator (Dominey 1983; Donaldson 1984; Brunton 1990), and to perform various sudden movements towards and away from the predator (Curio et al. 1983; Pitcher et al. 1986; Regelman & Curio 1986; Francis et al. 1989). Mobbing can be performed by single individuals or cooperatively by several conspecifics simultaneously (Bildstein 1982; Magurran & Pitcher 1987), or even by numbers of heterospecifics (Altmann 1956). Mobbing can also be specifically centred upon protecting the nest or offspring (Curio & Regelman 1985; Curio 1987; Wallin 1987; Hogstad 1993; Martin & Horn 1993; Gill & Sealy 1996). The ways in which different areas of study investigate such anti-predator behaviours is also quite varied, perhaps reflecting differences in taxonomy, traditions and methods in the different fields, as well as the adaptive function of these different behaviours.

MOBBING BEHAVIOUR IN BIRDS

Some of the best examples of studying anti-predator behaviour come from such studies on birds (e.g. Impeken 1976; Kullberg & Lind 2002; Davies et al. 2004; Magrath et al. 2006). Ultimately these approaches have been integrated to create general frameworks that are meant to account for alarm signals specifically, and other vocalisations in general (Hoogland 1996; Owings & Morton 1997, 1998; Owren & Rendall 1997, 2001; Ryan 1998). However, what defines the work on birds in terms of anti-predator research is the extensive exploration of nest or brood defence using mobbing

behaviour, via techniques such as acoustic playbacks, live predators and dummy models placed in the field (e.g. Curio et al. 1984; Wallin 1987; Gill & Sealy 1996). Such brood defence studies have investigated many effects on mobbing effort, such as the effect of body condition of the parents (Hogstad 1993), the quality and number of young (Curio 1987), the differential investment between sexes (Johnson & Albrecht 1993; Martin & Horn 1993; Hogstad 2005; Požgayová et al. 2009), the effects of life history (Curio et al. 1985) and the local environment (Fisher et al. 2004). However, whereas the use of alarm calls here draws attention to the cooperative nature of such anti-predator behaviours (see above), nest defence is often viewed in terms of individual parental investment to increase reproductive success (Curio 1987; but see Shields 1984). However, mobbing and parental nest defence are largely treated as synonymous, and often necessarily cooperative between the two members of the pair in most species of birds (e.g. Horn 1968; Robertson & Biermann 1979; Shalter 1979; Weatherhead 1979; Andersson et al. 1980; Grieg-Smith 1980; Patterson et al. 1980). Mobbing in this context can obviously be considered parental care, because all the fitness benefits are direct in that it increases the reproductive output aspect of the mobber's individual fitness (Shields 1980). There are also studies that explore the potential cooperative benefits of parental nest defence. Indeed, since mobbing also occurs outside the breeding season in many species (Curio 1978), and since often more than a single bird or a mated pair of conspecifics (and even heterospecifics) will mob simultaneously (Horn 1968; Hoogland & Shermann 1976; Kruuk 1976; Nolen & Lucas 2009), it is unlikely that a simple direct benefit of parental investment can account for all aspects of cooperative mobbing behaviour. Given the costly nature of anti-predator behaviour, one would expect parents to have specific responses to specific threats, for example if the type of predator is a threat to themselves or to their offspring. Thus, selection should result in a level of defence that is a balance between the benefit to the current brood and the survival of the parent and future reproductive success (Trivers 1972; Montgomerie & Weatherhead 1988). Such variable behaviour correlated to risk is well documented, not just in terms of different times in the season (e.g. before and after hatching, or with brood aged; Erpino 1968; Barash 1975; Curio 1975; Weatherhead 1979; Greig-Smith 1980; Biermann and Robertson 1981; Merritt 1984; Shields 1984), but also in terms of different types of predators (Kruuk 1964; Lemmetyinen 1971; Curio 1975; Greig-Smith 1980; Patterson et al. 1980; Buitron 1983; Gochfeld 1984; Brunton 1990; Sordahl 2004; Redmond et al. 2009). Given such important variables in relation to anti-predator behaviour, it is necessary to take into account the particular situation that a study was conducted in. There have traditionally been several adaptive hypotheses that might explain cooperative nest defence and/or mobbing behaviour, and below follows a quick review of the main ideas here (for specific hypotheses focused more upon mechanisms, see Curio 1978).

By-product mutualism: This is where cooperative behaviour does not incur a net cost to the donor (i.e. the first individual to mob). The benefits from this donor to the receiver (i.e. other individuals not mobbing) are merely a by-product of the donor's selfish behaviour to improve its own fitness (i.e. mobbing is profitable for that one first individual, even if no-one else joins in). The simplest example of such by-product mutualism is perhaps the selfish herd or dilution effect (Hamilton 1971), where individuals come together and thereby reduce each other's individual risk of predation by their sheer number. Another example of relevance to mobbing is the confusion effect (Miller 1922; Hoogland & Sherman 1976; reviewed in Jeschke & Tollrian 2007; Tosh et al. 2009), where by all moving unpredictably together a group of prey can reduce the per capita rates of predation by reducing the efficiency of predator attacks. The important point about all by-product mutualisms is that there is no incentive to cheat. However, compared to other theories concerning the evolution of cooperation, by-product mutualism has not been subject to much research in itself (but see Olendorf et al. 2003; Eberle & Kappeler 2008). There has not been much experimental testing of the mechanisms of by-product mutualism in mobbing and cooperative nest-defence. An exception here exists within the fish predator inspection literature, where one can find some studies in support of simple by-product mutualism. Note, however, that there has been some controversy in this case (e.g. Connor 1995, 1996; Milinski 1996) concerning the alternative possibility of reciprocal altruism (see below) in cooperative predator inspection behaviour. The by-product mutualism benefits of merely being in a group have, however, been thoroughly documented. Not only are larger groups more effective at detecting approaching predators (Pulliam 1973; Godin et al. 1988; Cresswell 1994), but predation risk is significantly reduced with increased group size (Magurran & Pitcher 1987; Krause & Ruxton 2002; Caro 2005).

Reciprocal altruism: This is where the costly actions of a donor benefit a receiver (typically an unrelated conspecific) in return for future reciprocation by that individual. Most important in this hypothesis is that the behaviour must be contingent: the help is given because of a future expectation of reciprocation (Trivers 1971). Such reciprocity has been shown to be evolutionarily stable under certain conditions using repeated play in a meta-game between neighbours (Axelrod & Hamilton 1981). The most prominent reciprocal strategy explored in the literature is Tit-For-Tat (TFT) (Axelrod & Hamilton 1981; Axelrod & Dion 1988). A TFT strategist always responds to its partner by mirroring their last action, whether it was altruistic or selfish. Thus, reciprocity makes the pay-off from cooperation frequency dependent and stabilizes a cooperative population against invasion by cheaters once it has reached fixation (Getty 1987; Eshel et al. 1998). Despite its continued popularity with theoreticians, this hypothesis is effectively impossible to refute, because the recipient must be shown to fail to repay the donor to the same eventual level of fitness at any time the future. The problem here is that it is difficult to quantify the fitness value of apparently

altruistic behaviour and the same or different (apparently) altruistic behaviour when it is used in reciprocation. This is especially so when there are the required asymmetries in fitness between the two players, for example when factoring in the varying skill levels or abilities for group members to reciprocate (Seyfarth and Cheney 1988; Boyd 1992). There is also the problem of power relationships distorting any reciprocation within social groups, because dominant members may exploit or manipulate subordinates (e.g. disproportionate grooming of high-rank members by low-rank members in primates; Barrett et al. 1999). The problem of expecting or even demonstrating a truly reciprocal exchange becomes worse with the increased complexity of life-long social associations, relatedness and altruistic interactions between several individuals occurring both directly and indirectly (Alexander & Borgia 1987). With regard to cooperative nest defence, there are some studies that claim support the hypothesis of reciprocal altruism (Beletsky & Orians 1987, Olendorf et al. 2003). However, despite these and numerous examples of the apparent use of TFT-like strategies in a variety of species (Packer 1977; Wilkinson 1984; Milinski 1987, 1990; Dugatkin 1991, 1996; Godard 1993), there is still controversy over the importance of reciprocal strategies in the maintenance of cooperation in non-human vertebrates (Curio 1978, Masters & Waite 1990; Connor 1992, 1996; Milinski 1996; Russell & Wright 2009), and severe criticisms have been raised against the hypothesis itself as being unfalsifiable.

Kin selection: This is where the costs to the donor are less than the benefits to the recipient taking into account the relatedness between the two, and hence there exists an indirect fitness benefit to the donor in performing the apparently altruistic act (Hamilton 1964). According to this hypothesis, the stability of cooperative mobbing should depend on kinship and the adaptive and even mutual protection of relatives, because including indirect fitness benefits reinforce the by-product mutualism benefits (see above). In contrast to reciprocal altruism, it is relatively straightforward to critically test kin selection as the mechanism through which cooperation can evolve and remain stable. With regard to mobbing, many studies that effectively support the kin selection hypothesis involve nest defence as parental investment, and there is recent evidence that extra-pair paternity reduces anti-predator behaviour (Trnka & Prokop 2010), but there is also work or relevance here on distress vocalisations, which are related to mobbing or alarm calls. In such studies researchers capture an individual measure the level of distress calls and the response of other individuals to its distress screams. Much of the work on distress screams, involves a possible interspecific function (reviewed in Rohwer et al. 1976; Chaiken 1992; Venuto et al. 2001; Neudorf & Sealy 2002), but there are a number of studies that test for kin selection in distress calls. For example, since there is sometimes a sex ratio bias in populations and the rare sex most often has the higher reproductive potential, there should be higher selective pressure for the rare sex to scream and thus be helped for reasons of kin selection by the common sex, than vice versa. Whilst Koenig et al. (1991) found no

such effect of sex or status in Acorn Woodpeckers (*Melanerpes formicivorus*), an effect of sex and offspring recognition has been found in other species (Chaiken 1992; Venuto et al. 2001). However, it appears that the function of distress screams is mainly as a form of predator manipulation (Perrone 1980; Koenig et al. 1991; Neurdorf & Sealy 2002) and/or predator startling (Conover 1994; Venuto et al. 2001; but see Wise et al. 1999). Mobbing rarely results from distress screams, although Chu (2001) found that heterospecifics were sometimes attracted to and mobbed a predator when phainopeplas (*Phainopepla nitens*) were screaming. Although it may simply be that birds use distress screams in general to locate and mob predators for their own benefits. What is noteworthy is that mobbing calls do in fact attract conspecifics or heterospecifics (e.g. Hurd 1996; Welbergen & Davies 2008). Thus it appears as though there is a real difference between a distress scream from a captured prey and mobbing calls in terms of function and the response of conspecifics and other species. Therefore, whilst kin selection does not appear to explain most distress screams, it may still well be an important selection pressure behind cooperative mobbing behaviour. Much of the literature that exists on cooperative mobbing involves cooperatively breeding species, which are largely groups of relatives. Such species make an obvious choice given their documented helping behaviour (Taborsky 1984; Brown 1987; Griffin & West 2002), and kin recognition (Pusey & Wolf 1996; Le Vin et al. 2010). These systems are also excellent for testing the other cooperative hypotheses, because by definition these species are at the extreme end of the spectrum of cooperation.

MOBBING IN COOPERATIVE BREEDERS

Cooperative breeders are species where helpers contribute effort to increase the reproductive potential of at least one breeding pair, at the cost of their own. Such systems are rare, with - for example - only 3% of avian species being categorized as such (Koenig & Dickinson 2004). Despite this they are found in many taxonomic groups, including birds (Stacey & Koenig 1990), mammals (Eberle & Kappeler 2006), invertebrates (Field et al. 1999) and fish (Taborsky & Limberger 1981). There has been a considerable research into different adaptive explanations for cooperative breeding, but only a few studies have been conducted on mobbing behaviour. Maklakov (2002) found that differences in snake-directed mobbing effort by Arabian babblers (*Turdoides squamiceps*) were correlated with differences in sex and rank, as well as with reproductive stage of the group. Females mobbed longer than males, and subordinate group members mobbed longer than dominant group members (for raptor mobbing, see Anava 1992). Time spent mobbing snakes also increased when the group contained dependent fledglings, and decreased during this period as these fledglings grew and became more capable. In accordance with kin selection for the protection of

these young relatives, groups that were more closely related mobbed more than less related groups. Although this was perhaps because there was a confounding interaction between group structure and individual rank, and the increased mobbing in more related groups was due to there being more subordinates in family groups. There was a lack of an effect of group structure (i.e. family versus complex structured groups), and this was also found by Payne et al. (1985) in splendid wrens (*Malurus splendens*). However, the pattern of relative mobbing effort within groups differs a great deal between the different species studies. In Florida scrub jays, it was the dominants that mobbed snakes the most (Francis et al. 1989). In splendid wrens it was primarily the breeding female, with less but equal mobbing effort by the rest of the group (Payne et al. 1985). Finally, in noisy miners (*Manorina melanocephala*) there is a subtle division of labour within these complex social groups, with propensity to mob or provision at the nest being negatively correlated (Arnold 2000a, 2000b). The differences in mobbing effort found in the above studies may be attributed to the potential threat that different predators (and indeed the same predators) pose to the respective species (Arnold 2000a; Maklakov 2002). Predators also elicit varying types of responses from different demographics based on the potential threat different predators pose based on their mobility and armaments (e.g. Montgomerie & Weatherhead 1988; Brunton 1990; Sordahl 2004; Négrel et al. 2010). In context of this study it should be specified that snakes in general are known nest predators, but pose less of a threat to adults (Maklakov 2002; Négrel et al. 2010). As already mentioned and as exemplified in the cooperative mobbing literature, it is vitally important to understand the situation of the study species in order to examine the functions of mobbing in an study

A quick overview of how cooperative behaviour in different taxa differs, and how the researchers have taken vastly different approaches, suggests that it is unlikely that there are many common patterns to mobbing behaviour. However, by looking past the traditional nomenclature certain similarities have presented themselves. In general, a lot of mobbing is triggered by the detection or surveillance of a single or a small group of vigilant individuals. Subsequent to detection, a number of conspecifics are attracted (or recruited) to the potential predator to assess the level of threat and to commence the appropriate response: either harass or move the predator on, or escape to safety. The dynamics of this series of behaviours may be complex. However, recent work on stochastic dynamic modelling has presented an interesting and simple alternative to the traditional approach to the dynamics of mobbing behaviour.

STATE-DEPENDENT MOBGING BEHAVIOUR

In the past few decades stochastic dynamic modelling (SDM) has been used to explore adaptive state-dependent strategies in a whole host of different theoretical problems in behavioural ecology,

and with considerable success. For example, SDM has been used to study behaviours such as bird song to attract mates (Houston & McNamara 1987), fighting for food (Houston & McNamara 1988), chorusing (Lucas & Howard 1995), moulting schedules in migratory birds (Holmgren & Hedenström 1995) and oviposition decisions (McNamara et al. 1995). Bednekoff (1997) employed SDM to explore cooperative behaviour in the form of state-dependent sentinel behaviour, which is a system of turn taking in dedicated vigilance with cooperative groups of birds and mammals. This SDM showed that a stable sequence of sentinel behaviour is possible within groups when individual effort is functionally selfish and determined entirely by individual state (i.e. energy reserves gained from foraging). This therefore represents a pure by-product mutualism and does not require the kin selected protection of relatives, or score keeping within reciprocal alliances. Each group member simply switched from foraging to anti-predator sentinel behaviour whenever it was in their own self-interest to do so, as determined by being a high enough state and if any other group member was already acting as a sentinel (i.e. the marginal benefits of a second sentinel are assumed to be very low if there is already one sentinel in place). This remarkably simple and parsimonious approach allowed Bednekoff (1997) to predict that there should be a positive relationship between body mass and sentinel effort, and that there should be lower sentinel effort per individual in larger groups, even though the total sentinel effort in the group as a whole should increase. The interesting thing here is that more complex explanations for this apparently altruistic behaviour, such as relatedness effects of kin selection and turn taking in reciprocity, were predicted to have no influence above and beyond these state-dependent predictions. This simple yet elegant model soon received strong empirical support, including experimental manipulation of state in both birds and mammals (Clutton-Brock et al. 1999; Wright et al. 2001a, 2001b, 2001c).

The success of SDM in furthering our understanding of cooperative behaviours such as sentinel behaviour (Bednekoff 1997), suggests that it might allow us to more fully understand other cooperative behaviours with alternative dynamics. In most cooperative actions (e.g. cooperative provisioning of young, vigilance, etc), an increase in the effort by one player is best met by (incomplete) decreases in effort by all other players (i.e. a negative compensation reaction: Bednekoff 1997; McNamara et al. 2002). However, certain cooperative behaviours, such as predator inspection and mobbing, might contain a positive feedback dynamic. Essentially, an increase in the mobbing effort of one player reduces the (predation risk) costs and/or increases the (predator deterrence) benefits for all other players, and hence we should perhaps see positive compensation reactions (Bednekoff et al. in prep.). For simplicity, mobbing can be defined as cooperative anti-predator behaviour to move predators on from foraging areas (i.e. avoiding the complexities of offspring defence, etc). In other words, the predator is repelled or harassed by a group of prey animals until it is coerced into leaving the immediate foraging area. Intuitively, one would expect

mobbing to work like sentinel vigilance behaviour and be state-dependent. For example, it could be the case that being in a poor state makes an animal more desperate to remove the predator so it is more quickly able to forage in safety. It might also be predicted that lower state individuals are more agile (being lighter), and mob at greater levels due to reduced costs because they can avoid predators more easily than their heavier conspecifics (i.e. given mass-dependent flight costs in birds). Conversely, it could be argued that group members in a high state are the first to mob since they have a lot of energy to spare for mobbing activity and can afford to break off from foraging or even from just resting to do so. Either way, in the traditional way of understanding mobbing behaviour, one might postulate many potential ways that state determines individual mobbing effort. However, according to recent SDM (Bednekoff et al. in prep.), mobbing should actually be completely state-independent. This interesting, counter-intuitive prediction arises because once one individual starts mobbing, it is always beneficial for all others to join in. This is because the more individuals that mob the lower the potential risks to any additional individuals that join in (i.e. predation risk is diluted) and the greater the chances of driving the predator off. Indeed, it has been found in other studies that an increased number of individuals lead to more effective mobbing (e.g. Boland 1998; Krams et al. 2009). The proposed positive feedback of mobbing effort within cooperative groups therefore leads to a 'social cascade' where one individual mobbing inevitably leads to more individuals mobbing, which leads to further mobbing by everyone present, irrespective of individual state. Such counter-intuitive predictions are very useful; they allow us to really test the validity of any model, because it is unlikely that the predictions are supported unless the model is describing something close to the dynamic of such behaviours in the real world. It may even be the case that mobbing works this way in many different systems. Some fish appear to show a turn-based inspection moves as they approach a potential predator (e.g. Milinski 1987; Wilson & Godin 2010). This might therefore be an example of the positive feedback dynamic described by Bednekoff et al. (in prep.) rather than the previously reported game of reciprocity or mutualism between conspecifics (see above). This project will therefore provide the first critical test of state-independent mobbing behaviour in a social bird.

AIMS OF THE STUDY

This study will investigate state-dependence in cooperative mobbing behaviour of apostlebirds (*Struthidea cinerea*). By conducting standardized experiments using moving model snakes (and control observations using a stick), and video analyses to quantify individual mobbing effort, I plan to quantify the cooperative dynamics of mobbing behaviour in this group-living bird. I will substantiate this with individual body mass measurements for the birds before each of the trials, and I will investigate the influence of different between-subject effects (e.g. sex, relatedness, age, breeding status).

The hypotheses I will use as a framework are:

H1: Time spent foraging/standing close to humans after feeding stops will be negatively correlated to relative individual body mass.

H0: No correlation between foraging time and body mass (state), or between proximity to humans and body mass (state).

1: I predict that foraging behaviour is state-dependent during controls, confirming the measures of body mass as a relevant state variable.

H1: Individual mobbing effort will show no correlation with relative individual body mass (i.e. state-independence).

H0: A correlation (positive or negative) will exist between mobbing and measures of individual body mass.

2: I predict that mobbing is state-independent, which is an interestingly counter-intuitive prediction from recent stochastic dynamic models.

METHODS

STUDY SPECIES

The apostlebird (*Struthidea cinerea*) is a medium-sized (33 cm, 130 g), ground-foraging, sexually monomorphic passerine. Offspring of both sexes are philopatric, accounting for the majority of new recruits into established groups (87.4%), and these remain as helpers in their natal group well into adulthood (Chapman 1998; Woxvold 2004). Apostlebirds therefore breed cooperatively in groups of three to 20 birds that remain stable throughout the year, and may even fuse into larger winter gatherings in some areas (J. Wright pers. comm.). They are aggressive mobbers of many different heterospecifics, and may mob anything from snakes to ravens, whether or not they pose an immediate threat to adults, nests or fledglings. Apostlebirds are naturally lacking in neophobia, and most birds of the population ($n \approx 300$, 20 – 40 social groups) living at Fowlers Gap have been systematically tamed over several years after being individually colour-banded and bled for later genetic analysis. They are therefore easily persuaded to get on electronic balances for body mass measurement. Their tameness also makes it possible to set up novel items like cameras and a sheet for covering the dummy snake, etc. without undue disturbance to the foraging group.

STUDY SITE

The fieldwork aspects of this study were carried out during the breeding season September to December 2009 at Fowlers Gap a research and teaching facility of the University of New South Wales (<http://www.fowlersgap.unsw.edu.au/site.htm>). The station is located 112 km north of Broken Hill, NSW (latitude 31° 05' S longitude 141° 43' E). Vegetation consists of low shrubland communities dominated by saltbush, bluebush and copper burrs with scattered mulga and belah, and river red gums along the ephemeral creeks. The climate is typical of the arid regions of the Southern Australia with mild winters and hot summers and an average annual rainfall over the last 30 years of 240 mm.

EXPERIMENTAL METHOD

When the apostlebird group to be tested was spotted, a suitable open area for the trial was located: at least 25 m² with vegetation nearby (preferably on sides A and C, see Figure 1). The experimental area itself had to be flat and open with minimal vegetation or large rocks. A sheet (ca. 1 m²) was

laid down in the centre of the area to hide the entire rubber snake (or stick; see control protocol below). As Figure 1 shows, the snake model had a string attached behind the head, which extended to Observer 1 via a peg that was driven into the ground 2.0 m in front of the head of the snake. This would be the distance the snake would travel during the trial. Observer 1 held the end of that line, and wound it up to at a set pace around a standardized reel with a circumference of 5 cm in order to gradually move the snake over the 2.0 m during the period of the whole trial. Two pieces of fishing line were also tied to two of the corners of the sheet closest to Observer 2, who then held the ends of these lines ready to reveal the snake (or stick) at the beginning of the trial. Two tripods were set up with cameras mounted so that their collective field of view covered as much of the area as possible (including behind the starting position of the sheet – see Figure 1). For ease of video analysis later (see below), it was important to position the cameras at consistent heights and angles between trials. The area immediately behind and surrounding the snake's path was deliberately covered by both cameras.

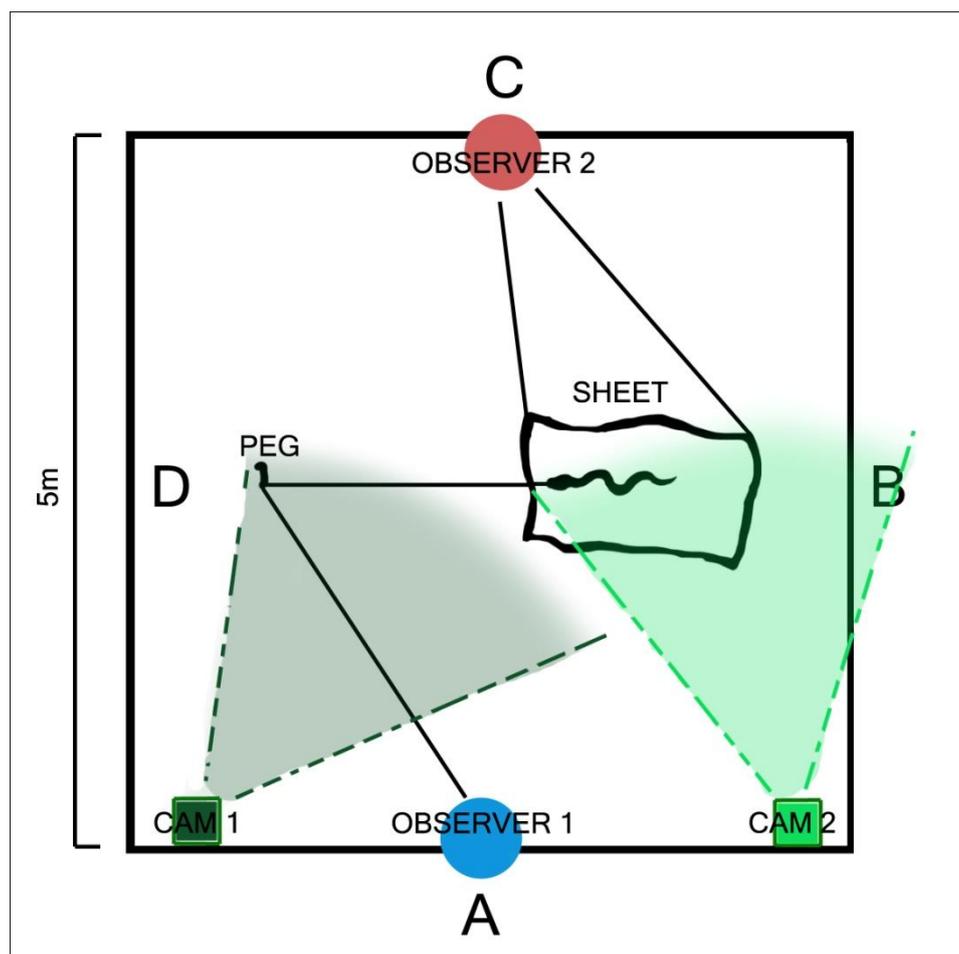


Figure 1. The setup of the experiment. Each side of the area is labelled (A-D) relative to the others. CAM 1 and CAM 2 are the video cameras, and the dotted lines represent their field of view. The rubber snake is underneath the sheet, and the full lines are the fishing lines from the snake (via the peg) and sheet corners to each observer respectively.

After everything was set up, the birds were attracted to the experimental area by whistling (the signal that was always given when observers feed these groups outside of the experiment). Both observers used top-pan electronic balances to collect body mass data (± 0.5 g) for as many individual birds as possible by feeding them very small pieces of bread from the hand when they stood still on the balance, as these birds had previously been trained to do. Not all birds in all groups had been fully tamed by the time of the early trials, and it was not possible to weigh every tame individual every time. We therefore made sure to get as many of the tamed birds on the balances as possible each trial within a limited time of 10 min in order to minimize the amount of bread consumed by any one individual and to prevent the group from dispersing too much prior to the trial. Mean number of body mass measurements overall was 62.6 % (± 31.2 %, ranging from 0 - 90 %) of the group. When body mass data had been collected, we waited for the birds to move away from the feeders and within a standard distance of the sheet (i.e. 50 % of the group < 1 m).

When the pre-trial conditions were met, the dictaphone held by each observer and the two video cameras were turned on, and the start of experimental trial was announced. Observer 2 then pulled the sheet at a steady and continuous pace (taking less than 5 secs in total) to reveal the snake or stick (depending on the type of trial). In experimental trials, as soon as the snake was revealed, it was pulled forward (every 15 secs) using continuous, small jerks and tugs (approximately 5 cm each) in between forward movements. The movement of the snake was deliberately controlled according to this set schedule and without reference to the behaviour of the birds around the snake. This was in order to standardize the stimulus within and between trials and groups. The pulling itself lasted the whole 5 min of the trial, and the snake did not reach the end of the track (2 m) before the 5 min were up.

During the 5 min trials, both the distance and relative position of each bird to the snake or stick was recorded in turn onto the dictaphones, including any aggressive or mobbing behaviours, as well as any other foraging, resting, preening or social behaviours. This was carried out continuously for every bird whenever the colour-bands could be seen. The aim was that at every 30 secs (i.e. for 11 time intervals per trial) we would be able to record point-time samples of distance and position to the snake or stick for every bird in the group. In addition, we would note their activity at the time, and how many vocalisations and behaviours of which kind they had done. The behaviours that were counted were number of pecks made at the snake, and the number of sudden, vertical jumps made when facing the snake. The vocalisations that were counted were two kinds of mobbing call: (a) a small clicking sound; and (b) a louder, more intense scratching sound. The point-time activities were entered separately from these vocalisations and behaviours, and were divided into natural

foraging, standing, preening, walking, watching snake. Natural foraging was defined as walking or standing with head lowered towards the ground. When the birds were standing still and facing it (< 4 m away), we defined their activity as watching the snake. Both standing and walking were defined as what the birds were doing when not actively involved in any other more obvious behaviour. We also entered the direction of walking (away from snake/stick, towards it, or parallel to it). Distance was measured in meters from the closest part of the snake or stick to the bird. The position of each bird relative to the closest part of the snake (or the stick) was recorded using the hours on the clock (e.g. '12 o'clock' = in front of the snake; '6 o'clock' = 'behind the snake'). At the end of 5 min in the experimental trials, the snake had reached the end of the track, and was carefully covered with the sheet again, the cameras and dictaphones were shut off and all equipment was packed up.

Everything was carried out in the same manner in experimental and control trials, although there was no string attached to the stick and it was not moved during the 5 min trial. The stick was essentially used to represent a familiar object under the sheet to control for the movement of the sheet, etc. Unlike the experimental trials where birds might mob the snake, the activities documented during control trials almost always included natural foraging or resting, preening, etc.

SCHEDULE

Data were collected from October 15th to November 21st 2009. The alternating sequence of control (stick) and experimental (snake) trials per group is shown in Table 1. Two groups of two observers each attempted to carry out trials on different groups through the sequence of morning or afternoon sessions. There were unavoidable gaps between 'consecutive' days throughout a sequence, for example due to bad weather or not being able to find a particular group. If on a particular day a morning session had been successfully carried out, then the matching afternoon session was also attempted on that same group. If it was not possible then the next earliest afternoon was to be used. The symmetrical nature of the experiment design was deliberately constructed so as to control for differences in time of day and time of season between experimental and control trials, including unforeseen delays with certain trials. Mean time of season (for control: 29th of Oct. \pm 11.2 days; for experiment: 29th of Oct. \pm 11.6 days) and mean time of day (for control: 12.03 \pm 4.79 hours after midnight; for experiment: 12.21 \pm 5.06 hours after midnight) were therefore very similar. We didn't manage to get all the groups (n = 6) completed before the season ended. Trials on two groups were incomplete (one went through only 6 trials, and one went through only 7).

Table 1. The sequence of trials per group over the span of 4 consecutive days (weather permitting). Each pair of trials is considered a trial set (4 trial sets in total).

Day	Morning	Afternoon
1	Control	Experiment
2	Control	Experiment
3	Experiment	Control
4	Experiment	Control

VIDEO ANALYSIS

Video analysis made it possible to combine and collate the data collected per trial by both observers on their data sheets and dictaphones (see above) into a single datasheet involving just the point-time sample data per 30 secs per bird in all groups. It also made it possible to confirm individual bird identifications by cross-referencing multiple identifications of the same individual on-screen at different times, based primarily on more reliable identifications (i.e. those made closest to the observer). Video analysis by a single observer also reduced any systematic bias or variation in the data collected by different observers. In order to minimize any temporal bias in the data collation, video tapes were also analysed in random order within and between groups.

Each birds was given a unique identification code that also corresponded to a group identity (3 birds moved groups during the period and therefore appear in more than one group in the data set). Not all birds could be positively identified during every scan sample (on average per scan $93.1\% \pm 18.5\%$, ranging from 0 – 100 %), and so in order to avoid loss of potential data it was necessary to create additional temporary ID codes for any unidentified birds for as long as they remained in view of the cameras. this allowed all behaviours per bird per group were attributed to the point-time interval in which they occurred, even if the individual involved could not be identified. All vocalisations and behaviours of interest during the preceding 30 secs were counted and attributed to an individual whenever possible in the subsequent scan sample data. When an alarm call during the trial was heard on the recording but the caller could not be identified, then it was attributed to a group specific ID code, but no single distance measurement could be associated with it. For distance comparisons in these cases we calculated the mean group distance at the following point-time interval in that trial, including those measurements for unknown bird IDs. This meant that we still had a rough estimate of how far away all birds were when an alarm call occurred that could not be attributed to a single bird.

In many cases, accurate distance data for every bird relative to the snake or stick was not available for every 30 sec interval per trial (i.e. $n = 2150$ out of 3904 instances), because individuals were outside the frame of the camera. In these instances, distance was entered as an average of minimum and maximum possible distance estimates given in the dictaphone commentaries by the observers at the time. Inclusion of these less precise distance estimates almost doubled the sample size for distance data to 3746 out of 3904 instances. Therefore, despite the relatively low precision of these individual estimates, this full data set including all distance measurements and estimates provided a much more complete overall picture of what happened during the trials.

GENETIC ANALYSIS

Blood samples were collected from all birds when originally captured as part of the wider field project 2003 – 2010. Sex was determined using the molecular methods described by Fridolfsson and Ellegren (1999), and all birds were typed using a set of 13 polymorphic microsatellite loci. Nine of the most variable and informative loci were then used for kinsgroup analysis, with four loci being dropped due to high rates of null alleles. The genetic data was calculated from the genotypes of 438 birds captured from 2005 – 2009. Allele frequency data were used to calculate pair-wise relatedness values between individuals in each group using KINGROUP v. 2 (Konovalov et al. 2004), with significance calculated based on the ratio required to exclude 95 % of 1000 simulated pair-wise comparisons. No bias correction was applied (correction assumes that birds in groups are more related to each other than within the population as a whole). When compared against known (i.e. mother-offspring) relationships, these estimated genetic relatedness values were shown to have an accuracy of $\pm 2\%$ (M. Warrington, unpublished data).

DATA ANALYSIS

Mixed effects models were used to assess the different variables that could affect individual distance from the stick/snake at the different time-intervals per trial. The models controlled for multiple observations via the random effects of individual identity (nested within group identity) and trial identity (nested within group identity). The different fixed effects included the between-subject effects of genetic relatedness (as a mean value per individual to all members of the group); minimum age (estimated based on date of first capture); breeding status (breeder vs. helper); and sex. Body mass represents a fixed effect that has both between-subject variance (i.e. mean mass per individual over all trials combined) and within-subject variance (i.e. between different trials per

individual). In order to assess state-dependence, it was necessary to split these two aspects of body mass into separate variables. We therefore followed the within-subject centring method described in van de Pol & Wright (2009) and calculated the mean body mass for each bird overall (i.e. the between-subjects effect) and subtracted it from each body mass value per bird per trial to quantify the variance around the mean for each individual (i.e. the within-subjects effect). Habituation (i.e. birds acclimating to the experiments and losing interest in mobbing) could potentially affect the results of this study, and so the systematic fixed effect of trial 'order' was tested for, and this was done over and above the random effect of trial identity (nested within group) mentioned above. Backwards elimination of non-significant interactions was used to simplify final mixed model structure. However, to avoid the inherent problems of multiple-testing with this approach (see Mundry & Nunn 2009; Forstmeier & Schielzeth 2011), we present only effects that were consistently significant both in full models and after non-significant interactions were gradually removed. We therefore also present more or less full models throughout the results. When comparing between-subject models we were mindful of their relative Akaike information criterion (AIC) values in order to balance the models' accuracy (goodness of fit) with their complexity (number of parameters). Such models were tested with maximum three between-subject variable at a time so as to not lose too many degrees of freedom. The response variable 'distance' was log transformed to normalise it, and all subsequent analyses were performed with this transformation implemented. All analyses were carried out using SPSS v. 16.0, with two-tailed tests and a critical P-value of 0.05 applied throughout.

RESULTS

DISTANCE AS MEASURE OF MOBBING

To test if distance represented a good estimate of mobbing effort, we compared the number of mobbing vocalisations and activities with the distance in individual birds from the snake (or stick). Distance as measure during the mobbing period was indeed uniquely associated with mobbing behaviours (Table 2). The two types of mobbing vocalisations were similar in their distance pattern, so they were combined into the “alarm calls” category shown in Table 2, which includes only cases where identified birds at precisely known distances were known to have given calls. The same effect of distance was also evident when calls came from “unknown” callers (see Methods), with about half of the calls (67 out of 123) being given by a bird when the mean group distance < 2 m. As mean group distance increased, the number of calls made by a bird decreased (group mean distance of each increasing (2 m long) distance category had 22, 17, 13 and 4 calls made by birds, respectively). Therefore, distance (log-transformed) will be used as a more detailed measure of mobbing effort in all subsequent analyses.

Table 2. The distribution and total number of alarm calls (n = 129), by known callers, given per 30 secs time interval during all experimental trials across all groups, divided by distance into half-meter categories. The 2 alarm calls in the > 3.0 m category were made at 9 m and 16.5 m.

Alarm calls (#) per 30 secs	Distance (m)						
	0.0 – 0.49	0.5 – 0.99	1.0 – 1.49	1.5 – 1.99	2.0 – 2.49	2.5 – 3.0	> 3.0
1	18	4	3	2	3	2	2
2	5	4	0	0	2	0	0
3	1	4	0	1	0	0	0
4	0	2	0	0	0	0	0
5	0	1	0	0	0	0	0
6	0	1	0	0	0	0	0
7	1	0	0	0	0	0	0
8	0	1	0	0	0	0	0
9	0	0	1	0	0	0	0
12	1	0	0	0	0	0	0
Sum total	50	51	12	5	7	2	2

WITHIN-INDIVIDUAL DIFFERENCES IN DISTANCE

Distances varied a lot with individual, group and the particular trail itself, and so these were included as random effects in mixed models (see Methods) to produce the residual values shown in Fig.2. Paired t-tests on individual differences in these values between sets of control and experimental trials (Table 3) revealed significant differences in the distances per individual (see Figure 2, and Table 3). At the beginning of the trial ($s = 0$), there was no significant difference between the two types of trials, as expected, given that this measurement was taken just before the removal of the sheet with the criterion of 50 % of the birds within < 1 m (see Methods). Subsequent to this, birds in control trials gradually increased their distance from the control stick as time progressed, essentially dispersing more quickly to forage elsewhere. In experimental trials, due to mobbing behaviours that attracted birds to the model snake (see above), the same birds stayed significantly closer than during control trials from 30 – 150 secs (i.e. hereafter the “mobbing period”). However, between 180 – 300 secs (i.e. hereafter the “foraging period”) all birds were no longer engaged in mobbing behaviours, and although they were just foraging they kept even farther away from the snake during the experimental trials than they did the stick during controls. It should be noted that at both 120 secs and at 240 secs the differences between controls and experiments were non-significant. This was probably due to chance, since these time-intervals both are situated within other significant time-intervals that were consistent in their direction and effect size. In addition, the 120-second interval is close to the end of the mobbing window, which may have made that time-interval more prone to becoming non-significant. We therefore felt confident in splitting the data into the two aforementioned periods.

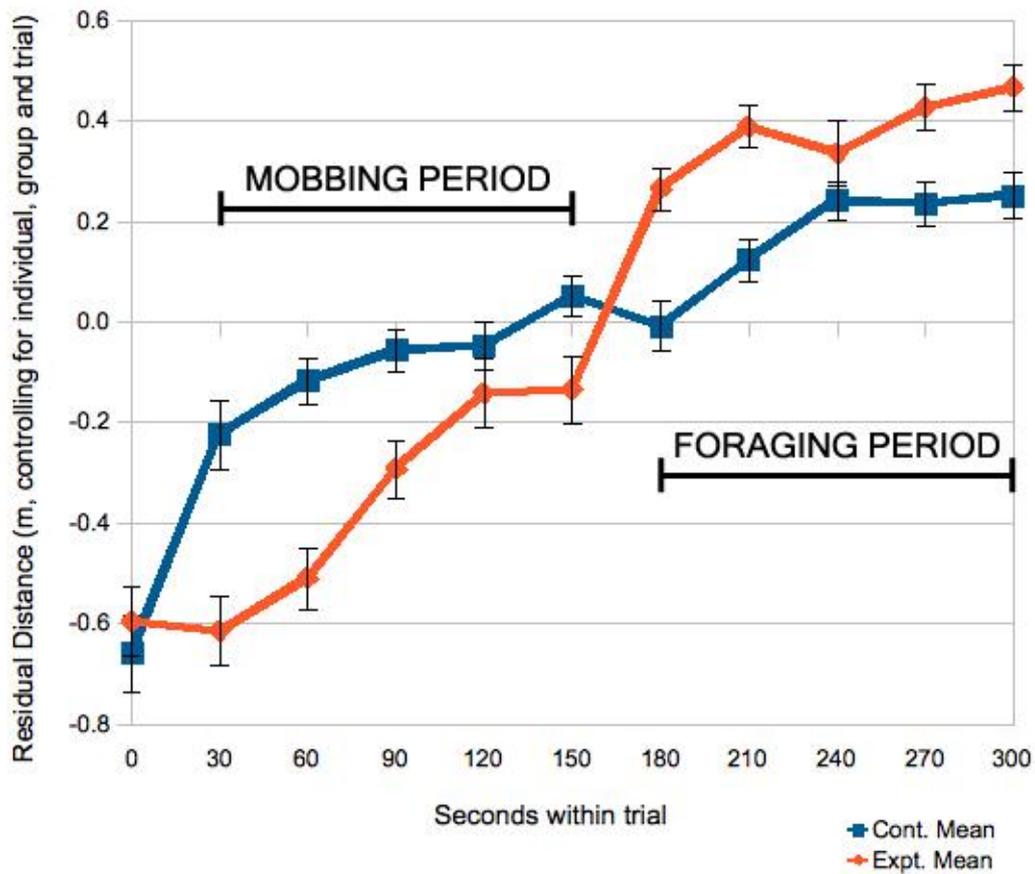


Figure 2. Mean log distance (\pm SE) per scan per individuals during control and experimental trials. Residual values are shown from mixed effects model containing only individual (within group) and trial (within group) as random effects. The differences between control and experimental trials (see Table 3) show a clear split into two distinct periods – the ‘mobbing period’ (30 – 150 secs) and the ‘foraging period’ (180 – 300 secs).

Table 3. Results from a series of separate paired t-tests on the mean distances per individual between control and experiment trials. ‘Start’ area designates the initial time-interval when distances were standardized before trial began. The birds stayed significantly closer to the snake during the ‘mobbing period’ (30-180 secs) and then switched to being further away during the ‘foraging period’ (180 – 300 secs) – see Fig.2.

Time	0	30	60	90	120	150	180	210	240	270	300	
t-value	-0.61	3.88	4.97	3.56	1.18	2.28	-4.64	-4.78	-1.24	-3.01	-3.11	
df	44	48	48	50	48	53	54	53	54	53	52	
P-value	0.547	<0.001	<0.001	0.001	0.245	0.026	<0.001	<0.001	0.220	0.004	0.003	
	START	-----MOBBING PERIOD-----						-----FORAGING PERIOD-----				

A mixed effects model of all these data was used to determine how further analyses should proceed (Table 4). Type of trial (i.e. experiment or control) had no significant effect overall, or in two-way interactions with body mass, order or time. Trial order (i.e. effect of the sequence of trials) had a complex effect that was significant both alone and in all interactions with time and body mass, including the three-way interactions with time and body mass. In other words, the within-individual differences in distance within trials, between controls and experiments, were changing for each trial set. This all shows that there was a very specific effect of habituation that varied within and between trials in a complex way, but that it did not vary between control and experimental trials. These two crucial but rather complex results indicate that the best procedure would be to split up any further analyses into two parts: one model for control trials and one for experimental trials. It would then be possible to look at how distance varied within each type of trial, and identify the origins of the effect of order, to see if it affected our results. The complicated three-way interactions could also be more closely scrutinized by splitting the data into separate models. In addition, these models were split into the mobbing and foraging periods to see if different effects were at work within trials.

Table 4. A mixed effects model of the full data set, with three-way interactions. Significant fixed effects are shown in bold. The time variable expresses secs from the start of trials (0 – 300 secs). Type of trial expresses controls versus experiments. Order expresses the sequence of trials (1 – 8) as its own effect. Body mass is the values as measured before trials.

Variable	df	F-value	P-value
Intercept	1, 828	1.50	0.221
time	1, 1995	7.35	0.007
type of trial	1, 1714	1.00	0.317
order	1, 1965	10.62	0.001
body mass	1, 791	5.29	0.022
time*body mass	1, 1995	3.35	0.068
type of trial*body mass	1, 1987	2.43	0.119
order*body mass	1, 2026	11.02	0.001
type of trial*time	1, 1984	1.26	0.262
order*time	1, 1986	10.62	0.001
type of trial*order	1, 1337	0.05	0.833
type of trial*order*time	1, 1984	9.50	0.002
type of trial*time*body mass	1, 1983	3.90	0.048
type of trial*order*body mass	1, 1770	0.06	0.813
order*time*body mass	1, 1986	9.76	0.002

ASSESSING STATE-DEPENDENCE

In contrast to the single large model (above), using absolute body mass (as measured) in split mixed models yielded largely non-significant results (Table 5) – note that for simplicity most between-subject variables have been left out at this stage (see below). In these smaller models the effects of order almost completely disappeared, only being significant in an interaction with time during the foraging period in control trials. Such variable effects of order might explain the complex interaction in Table 4, and show that habituation effects were only evident in these data in the relatively minor effect of the shallow increase in distance over time during the foraging periods and how this changed over the course of successive control trials. Further examination revealed that this effect was caused by the first control trial (out of four), when individual movement was on average more extreme than the later trials; staying closer during the mobbing period, and moving farther away during the foraging period. This could be due to some initial response to the trial set up, but it's difficult to determine. Birds in the other three control trials had more uniform distances from the stick at a given time. Overall this suggests that habituation was not biologically important in this study. .

In order to explore body mass in more biologically meaningful detail, we separated body mass into within- and between-individual variation (see Methods). Models including these new non-confounded body mass variables provided clear and significant results (see Table 6). In the control trials during the mobbing period, within-individual variation in body mass (state) had a significant negative effect on distance (Table 6a; Fig.3), suggesting that individuals in relatively poor state moved away to forage more quickly during control trials. During experimental trials, there was no such effect, suggesting the mobbing was not dependent on state in the same way as foraging. There was a significant positive effect of within-subjects variation in body mass in the foraging period during experimental trials, but not during control trials (Table 6b; Fig.3). In this case, heavier individuals moved further away from the snake (but not the stick) when foraging during the later stages of the trials. There was also a minor interaction in the effect of mean between-subjects variation in body mass and time within the trial for mobbing periods of experimental trials (Table 6a). Given that this might reflect differences between group members in mobbing effort, this will be explored in the next section on between-subject effects.

Table 5. Results from four linear mixed models, for control and experimental trials, for all distance data during (a) the mobbing period and (b) foraging period, respectively. In these models, body mass is tested as it was measured before each trial, with no alternation. The effect of trial number is also included.

Trial type	Variable	df	F-value	P-value	df	F-value	P-value
Control	Intercept	1, 265	0.46	0.497	1, 458	0.01	0.911
	time	1, 372	0.40	0.527	1, 416	0.27	0.602
	body mass	1, 263	2.65	0.105	1, 448	0.22	0.637
	order	1, 371	1.43	0.232	1, 340	0.87	0.352
	time*order	1, 372	1.13	0.288	1, 416	4.61	0.032
	time*body mass	1, 372	0.56	0.455	1, 416	<0.01	0.974
	order*bm	1, 384	2.21	0.138	1, 380	0.96	0.329
Experiment	Intercept	1, 340	1.64	0.201	1, 461	0.24	0.628
	time	1, 436	0.61	0.435	1, 425	0.09	0.770
	body mass	1, 331	0.11	0.296	1, 447	<0.01	0.998
	order	1, 412	<0.01	0.996	1, 392	1.73	0.190
	time*order	1, 433	0.72	0.397	1, 424	1.71	0.192
	time*body mass	1, 436	1.96	0.162	1, 424	0.46	0.496
	order*bm	1, 423	0.07	0.799	1, 447	1.44	0.230

Table 6. Results from four linear mixed models, for control and experimental trials, for all distance data during (a) the mobbing period and (b) foraging period, respectively. Here the body mass variable has been split into two different levels of aggregation: within-individual variance, and between-individual variance (mean mass). Significant effects are shown in bold.

Trial type	Variable	df	F-value	P-value	df	F-value	P-value
Control	Intercept	1, 106	5.53	0.021	1, 445	0.32	0.573
	Mean mass	1, 103	2.26	0.136	1, 442	1.30	0.256
	w/ ind. mass	1, 410	10.14	0.002	1, 427	0.32	0.575
	time	1, 376	3.82	0.051	1, 419	0.89	0.347
	time*w/ ind. mass	1, 375	3.13	0.078	1, 419	0.03	0.870
	time*Mean mass	1, 377	4.69	0.031	1, 419	0.49	0.484
Experiment	Intercept	1, 226	6.44	0.012	1, 446	0.31	0.577
	Mean mass	1, 221	3.38	0.067	1, 44	<0.01	0.949
	w/ ind. mass	1, 459	0.83	0.364	1, 434	4.52	0.034
	time	1, 435	1.84	0.176	1, 425	0.01	0.908
	time*w/ ind. mass	1, 431	0.94	0.333	1, 424	3.51	0.062
	time*Mean mass	1, 435	3.30	0.070	1, 425	0.01	0.922

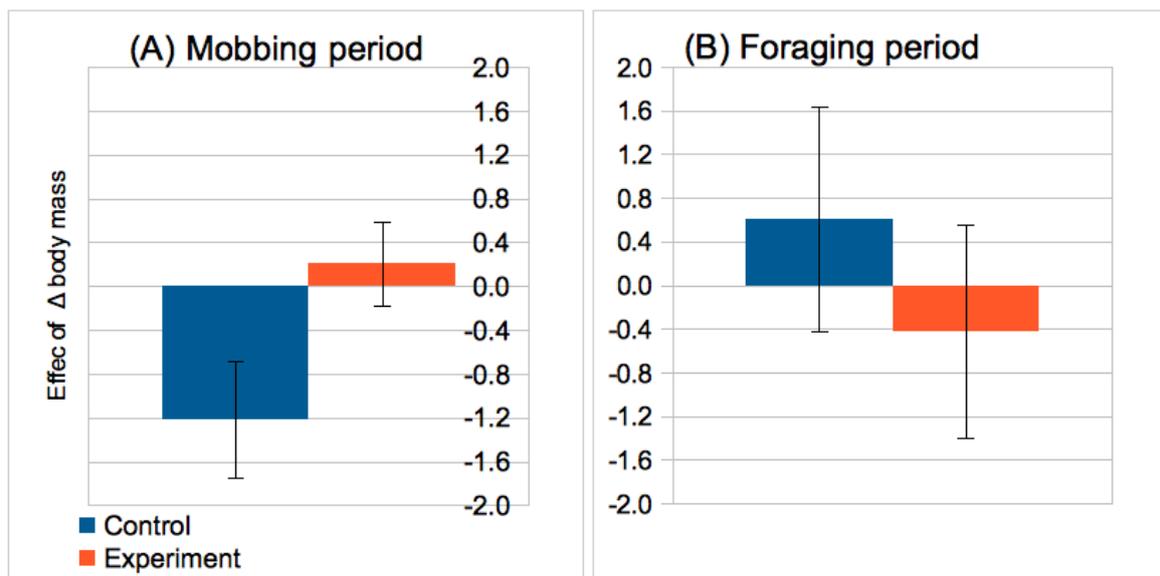


Figure 3. The mean (\pm SE) effect sizes (i.e. slopes of the regressions) for within-individual variation in body mass on distance from the snake or stick during: (a) the mobbing period; and (b) the foraging period. There was a clear significant (negative) difference from zero during the mobbing period of control trials, and to a lesser extent a (positive) difference from zero during the foraging period of experimental trials - see Table 6 for the results of the mixed models from which these effect sizes were derived.

BETWEEN-SUBJECT EFFECTS

When testing for potentially covarying between-subject effects, there is a danger of conflation, especially in a data set like this with relatively small numbers of individuals. For example, heavier birds on average might also be older birds, and we know that breeders are likely most likely to be older individuals as well. Therefore, all between-subject variables were included in a association-matrix - note that for the bivariate variables (e.g. breeder vs. non-breeder; males vs. females) it was necessary to perform Mann-Whitney U-tests instead of correlations (see Table 7). Most key variables turned out to be unassociated, although mean individual body mass was positively, almost significantly, associated with mean genetic relatedness to the rest of the group. Similarly, age and sex were positively and almost significantly associated, with males (mean age = 4.1 ± 1.8 , ranged from 1 – 8 years old) being on average older than females (mean age = 3.1 ± 1.7 , ranged from 1 – 8 years old). As expected, breeding status was positively associated with minimum age. We therefore need to bear in mind these particular associations between independent variables when constructing all subsequent models to explore between-subjects effects on mobbing effort.

Table 7. Associations between variables values per individual, either as Pearson correlations (for continuous variables) or Mann-Whitney U-tests (for bivariate variables). Significant relationships are shown in bold. Relationships close to $P = 0.05$ are shown in regular black.

		Mean body mass	Relatedness	Minimum age
Mean body mass	Pearson correlation	1	0.29	0.077
	P-value		0.063	0.629
	N	42	42	42
Relatedness	Pearson correlation	0.29	1	-0.157
	P-value	0.063		0.243
	N	42	63	57
Minimum age	Pearson correlation	0.077	-0.157	1
	P-value	0.629	0.243	
	N	42	57	63
Sex	Mann-Whitney U	205	344	281
	P-value	0.733	0.445	0.067
	N	42	57	57
Breeding status	Mann-Whitney U	53	215	55
	P-value	0.125	0.675	< 0.001
	N	42	57	57

The results involving between-subject effects produced varying results (summarised in the best models in Table 8), depending on which variables were included or excluded from the mixed models, and also on the complexity of the model. Sex was the only variable that showed consistently significant effects on distance in simple and more complex models. Breeding status had some significant effects when included in models that included the variable of sex. However, the significance for breeding status disappeared entirely in other models. Breeding status was therefore excluded from the final between-subject model (see Table 8) as it was inconsistent in its statistical significance. Mean body mass ceased to show the interaction shown in Table 6a, suggesting that this previous result was due to other between-subjects differences (perhaps related to the sex differences) than mean body mass *per se*. The two within-subject body mass effects that were significant in previous models (Table 6) remained significant, and the lack of any interactions with these between-subjects effects show that any state dependence (see above) was universal to all group members equally.

Table 8. Results from four linear mixed models, for control and experimental trials, for all distance data during (a) the mobbing period and (b) foraging period, respectively. These models are similar to those in Table 6, but now include also the effect of sex. Significant effects are shown in bold.

Trial type	Variable	(A) MOBGING PERIOD			(A) FORAGING PERIOD		
		df	F-value	P-value	df	F-value	P-value
Control	Intercept	1, 106	3.46	0.066	1, 444	0.22	0.637
	time	1, 370	1.78	0.183	1, 417	0.75	0.389
	sex	1, 121	9.80	0.002	1, 443	0.35	0.555
	Mean mass	1, 103	1.13	0.290	1, 440	1.10	0.296
	Δ body mass	1, 406	9.57	0.002	1, 426	0.32	0.574
	time*sex	1, 370	10.78	0.001	1, 419	0.13	0.723
	time*mean mass	1, 370	3.24	0.073	1, 418	0.03	0.857
	time*Δ body mass	1, 370	2.52	0.113	1, 417	0.40	0.528
Experiment	Intercept	1, 222	6.22	0.013	1, 442	0.35	0.554
	time	1, 432	1.69	0.194	1, 424	<0.01	0.941
	sex	1, 250	0.82	0.367	1, 447	0.53	0.466
	Mean mass	1, 216	3.22	0.074	1, 438	<0.01	0.970
	Δ body mass	1, 456	1.19	0.227	1, 433	3.95	0.047
	time*sex	1, 429	0.23	0.632	1, 424	0.70	0.405
	time*mean mass	1, 428	1.31	0.253	1, 423	3.01	0.084
	time*Δ body mass	1, 433	3.07	0.081	1, 424	0.02	0.898

GROUP LEVEL EFFECTS

Body mass and relatedness as variables were of high precision and range compared to other between-subject variables, and were therefore examined further. In the case of these variables, there could also be conflation due to between-group differences. Following the same procedure for within-subject centring, we calculated the new variables of mean relatedness and body mass per group, and centred their variance to produce individual values within each group. Correlations between these new variables showed that neither of the group level effects were conflated (within-groups: $P = 0.795$, $r = 0.041$, $n = 43$; and between-groups: $P = 0.192$, $r = 0.617$, $n = 6$), and so the final models could include all independent variables (see Table 9). Sex was included since it was significant in some places for previous models and because it is also a measure of between-subjects variance (i.e. within-group). Removing this variable did not strongly affect the highly significant results one way or another in general. However, the effect of sex becomes non-significant in the mobbing period during controls (compare with Table 8), and only group mean effects end up being significant in these group level models. This indicates that between-subject effects are less important as variables to explain mobbing effort in our data than the identity of the group itself, which could also mean that we have too low a sample set to further explore these types of models.

Table 9. Results from four linear mixed models, for control and experimental trials, for all distance data during (a) the mobbing period and (b) foraging period, respectively. The variables included here are at within-group or between group level of aggregation. Significant effects are shown in bold.

Type of trial	Variable	(A) MOBING PERIOD			(B) FORAGING PERIOD		
		df	F-value	P-value	df	F-value	P-value
Control	Intercept	1, 28	3.91	0.058	1, 46	12.18	0.001
	time	1, 533	0.58	0.446	1, 597	12.22	0.001
	sex	1, 178	0.53	0.446	1, 612	0.82	0.366
	Δ relatedness	1, 174	2.90	0.090	1, 612	3.56	0.060
	Δ body mass	1, 180	1.57	0.212	1, 612	0.11	0.740
	Mean mass	1, 28	4.90	0.035	1, 45	13.26	0.001
	Mean relatedness	1, 25	1.02	0.321	1, 35	3.54	0.068
	time*sex	1, 532	2.22	0.137	1, 587	0.39	0.531
	time* Δ relatedness	1, 531	0.15	0.698	1, 588	2.79	0.095
	time* Δ body mass	1, 531	3.43	0.064	1, 587	<0.01	0.980
	time*mean mass	1, 533	0.68	0.411	1, 597	11.61	0.001
	time*mean relatedness	1, 531	20.83	<0.001	1, 586	9.34	0.002
	Experiment	Intercept	1, 34	5.31	0.027	1, 65	1.41
time		1, 544	5.11	0.024	1, 551	0.12	0.733
sex		1, 253	0.19	0.668	1, 568	1.87	0.172
Δ relatedness		1, 241	0.11	0.742	1, 563	0.34	0.558
Δ body mass		1, 265	<0.01	0.924	1, 569	0.37	0.544
Mean mass		1, 34	4.25	0.047	1, 64	2.17	0.146
Mean relatedness		1, 30	<0.01	0.932	1, 51	8.39	0.006
time*sex		1, 543	0.04	0.850	1, 549	2.60	0.107
time* Δ relatedness		1, 540	0.19	0.660	1, 549	0.63	0.427
time* Δ body mass		1, 544	0.03	0.875	1, 549	0.17	0.678
time*mean mass		1, 544	5.79	0.016	1, 550	0.08	0.772
time*mean relatedness		1, 545	0.16	0.689	1, 548	1.35	0.246

DISCUSSION

The detailed behavioural data showed that mobbing calls and other anti-predator behaviours strongly reflected how far away (or rather, how close) the individual birds were from the snake. The benefit of choosing distance as the metric of interest is its inherent objectivity. Rather than counting number of mobbing bouts or closest distances approached within a mobbing bout, as previous studies have done (e.g. Arnold 2000a; Ostreiher 2003; Krams et al. 2009), it was possible to continuously and accurately estimate distance and leave relatively little room for subjective interpretation. Probably as a consequence of the lack of dependent young group members to protect, the mobbing effort during the 2009 breeding season was less intense than anticipated from previous observations. However, using distance as a proxy for mobbing effort made it possible to assess the more subtle aspects of low intensity mobbing. It also allowed us to directly compare distances during controls versus experiments, since distance was also a good metric for identifying the switch from mobbing to foraging behaviour.

In the ‘mobbing period’ during controls, birds move away from the centre of the area to forage, and they did so in relation to their state (within-individual variation in body mass). So, when the birds were attracted to the open area for weighing before each trial, they all started off more or less in the centre close to the stick with limited foraging opportunities. When the trial started and the sheet was removed, these habituated birds were not disturbed, and simply ignored the stick and had no reason to stay in the open space since there was no longer any food being given out. They started to forage, with relatively lighter birds moving away to better foraging areas (i.e. amongst bushes and trees) faster than relatively heavier birds.

As the control trials continued on into the ‘foraging period’, the movement away from the centre of the trial area gradually tapered off, probably as a result of the increasing larger foraging areas and therefore prey availabilities provided by each move further away. The strong state-dependence that was at work during the control trials had completely disappeared by the ‘foraging period’. So, once the birds had moved out to these foraging area (according to their state), there was no need for lighter birds to move further away faster during the second half of the 5 minute trial. These results touch upon the interesting idea that state-dependence might dictate group movement when foraging (and especially switches between foraging patches), which has recently gained momentum in both theory (e.g. Rands et al. 2004; but see also Rands & Johnstone 2006; Rands et al. 2008) and empirical studies (de Laet 1985; Black 1988; Hogstad 1988; Gotceitas & Godin 1991; Fischhoff et al. 2007). Apostlebirds, being so easy to tame and weigh, might in fact be an ideal

species for further research on this topic, and some of the highly detailed data collected in this study could perhaps be utilized in the future to test some of the relevant models (e.g. effect of nearest neighbours).

The main results of this study, however, obviously centre on the data during the snake mobbing trials. An unexpected benefit with having measured a less intensive mobbing effort overall was that we managed to capture whole mobbing bouts from start to finish, and to record the transition from mobbing behaviour into foraging behaviour in the presence of a predator (see Fig. 1). In contrast to the control trials, during the mobbing period in the experimental trials birds stayed close to the centre of the testing square (i.e. close to the snake), and there was no detectable state-dependence in any distances or movement away (see Fig. 3). As with the control trials, there was a change in how the birds behaved when the foraging period started. From 180-300 secs, the distance the birds maintained from the snake became weakly positively state-dependent, with the birds staying significantly farther away than they did during controls. Hence, only once the birds stopped mobbing and started to forage did their distance movements become state-dependent. The foraging behaviour of group-living species is known to be heavily affected by the presence of predators (Morgan & Colgan 1987; Verplancke et al. 2010). The state-dependence with distance during this foraging period of experimental trials could therefore reflect a strategy to minimize the risk of predation by the snake whilst foraging. There are studies that indirectly show state-dependence of take-off speed and flight performance (e.g. Metcalfe & Ure 1995; Kullberg et al. 1996; Lind et al. 1999), which translates to greater predation risk. Strangely enough, our results (see Fig. 3b) indicate a weakly negative relationship between distance and state, implying that lighter birds moved farther away from the snake than did heavier birds. It is unclear why this might be the case.

The exploration of between-subject effects yielded few positive results, perhaps because the sample size ($n=57$ individuals in 6 groups) was not large enough to properly reveal for these types of effects. Some obvious relationships were evident, such as breeding status being positively associated with minimum age. However, mean body mass was not correlated with minimum age as one would expect. This could be due to these groups containing very few 1 year old sub-adult individuals. Only the sex of the bird seemed to be a phenotypically fixed factor that really explained any variance in behaviour. There was a highly significant time by sex interaction that accompanied the significant effect of sex in the mobbing period in controls. Females initially stayed closer at the start of the trials, but they were soon at equal distance as the males. Given the lack of any correlation between sex and mean body mass, this result is unlikely to have anything to do with the females being underweight and thus in a poor state in general. The lack of strong between-subject effects in explaining mobbing effort does substantiate the idea of safe, selfish mobbing that always

benefits the members of a group to join in. It is also consistent with a previous test of state-dependence for sentinel behaviour in Arabian babblers (*Turdoides squamiceps*) where sex and dominance also did not affect the number of alarm calls given while being the sentinel (Wright et al. 2001c). Mobbing effort itself however has been shown to vary between sex and dominance (Maklakov 2002), and other studies have shown similar between-individual variance (e.g. dominance: Slagsvold 1985; age and sex: Graw & Manser 2007), so it remains possible that such variance exists in apostlebird mobbing as well. This study was designed to test within-individual effects of state, and so should therefore not be viewed as a definitive study on differences in mobbing effort between different classes of individuals. When group level effects were further examined, the effect of sex vanished, or was replaced by mean body mass and a relatedness interaction with time. At the group level, the sample size ($n = 6$) perhaps limits any meaningful tests. The specific characteristics of these particular groups probably mattered more than anything else, especially since it was only group mean effects that came up significant (and no within-group effects did).

There was a clear strong state-dependent effect on foraging effort, and state-independence in the mobbing effort of these same birds (see Figure 3). These results therefore suggests that the model by Bednekoff et al. (in prep.) is possibly correct in predicting state-independent mobbing behaviour. However, we did not observe any clear social cascade effect. The mobbing response was too weak and so all the birds did not join in at the same time, escalating the group mobbing effort (for effect of group size on mobbing, see e.g. Krams et al. 2009). However, one problem with the approach taken by this study is that it seems we have confirmed what should be a null hypothesis (i.e. that mobbing effort does not depend upon the state of a individual), which is not what statistical tests are designed to do. Having failed to find a significant effect, can we really conclude that mobbing effort is state-independent? A colloquial expression of this potential critique of our results is: “absence of evidence is not evidence of absence”. The fact that we failed to find an effect of body mass on mobbing effort does not necessarily mean that such an effect is not there to be found. In response to this, it is clear that strong state-dependence was found in foraging behaviour of the very same individuals within very similar circumstances (i.e. controls). Thus, if mobbing were state-dependent then this data set appears to have the statistical power to find it. Absence of state-dependence during mobbing therefore lends strong support for the model by Bednekoff et al. (in prep). However, future studies are clearly needed to properly substantiate this, and the presence of a positive feedback dynamic and ‘social cascade’ effect in cooperative mobbing effort.

State-dependence is pervading many fields of study in behavioural ecology. Its parsimony and generality makes it a convincing theory that explains many different kinds of behaviour. Additionally, stochastic dynamic modelling as a method for accurately quantifying and predicting the moment-by-moment decision-making of animals has been thoroughly supported by evidence. Our study builds upon the theoretical strength of the former, and the predictive strength of the latter, and the results point to a new way of viewing mobbing as a cooperative strategy.

REFERENCES

- Altmann, S. A. (1956). *Avian mobbing behavior and predation recognition*. Condor 58: 241-253.
- Alexander, R. D. & Borgia, G. (1978). *Group selection, altruism, and the levels of organization of life*. Ann. Rev. Ecol. Sys. 9: 449-474.
- Anava, A. (1992). *The value of mobbing behaviour for the individual babbler (Turdoides squamiceps) (in Hebrew)*. MSc Thesis, Ben Gurion University of the Negev, Beer-Sheva.
- Andersson, M., Wiklund, G., Rundgren, H. (1980): *Parental defence of offspring: a model and an example*. Anim. Behav. 28: 536-542.
- Arnold, K. E. (2000a). *Group mobbing behaviour and nest defence in a cooperatively breeding Australian bird*. Ethology 106: 385-394.
- Arnold, K. E. (2000b). *Cheats or specialists? Variable helping strategies in cooperative breeders*. Abstracts of 8th International Behavioural Ecology Congress, Zoological Museum, University of Zurich.
- Axelrod, R. & Dion, D. (1988). *The further evolution of cooperation*. Science 242: 1385-1390.
- Axelrod, R. & Hamilton, W. D. (1981). *The evolution of cooperation*. Science 211:1390-1396.
- Barash, D. P. (1975). *Evolutionary aspects of parental behavior: distraction display of the alpine accentor*. Wilson Bull 87: 367-373.
- Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., Hill, R. A. (1999). *Market forces predict grooming reciprocity in female baboons*. Proc. R. Soc. Lond. B-Biol. Science, Vol. 266, No. 1420: 665-670.
- Bednekoff, P. (1997). *Mutualism among safe, selfish sentinels: a dynamic game*. Am. Naturalist Vol. 150, No. 3: 373-392.
- Beletsky, L. D. & Orians, G. H. (1987). *Territoriality among male red-winged blackbirds. 1. Site fidelity and movement patterns*. Behav. Ecol. Sociobiol. 20: 21-34.
- Biermann, G. C. & Robertson, R. J. (1981). *An increase in parental investment during the breeding season*. Anim. Behav. 29: 487-489.
- Bildstein, K. L. (1982). *Responses of Northern Harriers to mobbing passerines*. J. Field Ornithol. 53: 7-14.
- Black, J. M. (1988). *Preflight signalling in swans: a mechanism for group cohesion and flock formation*. Ethology 79: 143-157.
- Boland, C. R. J. (1998). *Helpers improve nest defence in cooperatively breeding White-winged Choughs*. Emu 98: 320-324.

- Boyd, R. (1992). *The evolution of reciprocity when conditions vary*. In: Harcourt, A.H., de Waal, F.B.M. (Eds.), *Coalitions and Alliances in Humans and Other Animals*. Oxford University Press, Oxford, p. 473-489.
- Brown, E. D. (1985). *Functional Interrelationships Among the Mobbing and Alarm Calls of Common Crows (Corvus brachyrhynchos)*. *Zeitschr. Tierpsychol.* 67: 17-33.
- Brown, J. L. (1987). *Helping and Communal Breeding in Birds: Ecology and Evolution*. Princeton, New Jersey: Princeton University Press.
- Brunton, D. H. (1990). *The effects of nesting stage, sex, and type of predator on parental defense by killdeer (Charadrius vociferous) - testing models of avian parental defense*. *Behav. Ecol Sociobiol.* 26: 181-190.
- Buitron, D. (1983). *Variability in the responses of Black-billed Magpies to natural predators*. *Behaviour* 78: 209-236.
- Caro, T. (2005). *Antipredator Defenses in Birds and Mammals*. Chicago: University of Chicago Press.
- Chaiken, M (1992). *Individual recognition of nestling distress screams by European starlings (Sturnus vulgaris)*. *Behaviour* 120: 139-150.
- Cheney, D. L. & Seyfarth, R. M. (1990). *How monkeys see the world*. University of Chicago Press, Chicago. 377pp.
- Chu, M. (2001). *Heterospecific responses to scream calls and vocal mimicry by phainopeplas (Phainopepla nitens) in distress*. *Behavior* 138: 775-787.
- Clutton-Brock, T. H., O'Riain, M. J., Brotherton, P. N. M., Gaynor, D., Kinsky, R., Griffin, A. S., Manser, M. (1999). *Selfish Sentinels in Cooperative Mammals*. *Science* 284: 1640-1644.
- Connor, R. C. (1992). *Egg-trading in simultaneous hermaphrodites: an alternative to tit-for-tat*. *J. Evol. Biol.* 5: 523-528.
- Connor, R. C. (1995). *The benefits of mutualism: a conceptual framework*. *Biol. Rev.* 70: 427-457.
- Connor, R. C. (1996). *Partner preferences in by-product mutualisms and the case of predator inspection in fish*. *Anim. Behav.* 51: 451-454.
- Conover, M. R. (1994). *Stimuli eliciting distress calls in adult passerines and response of predators and birds to their broadcast*. *Behaviour* 131: 19-37.
- Cresswell, W. (1994). *Flocking is an effective anti-predation strategy in redshanks, Tringa totanus*. *Anim. Behav.* 47: 433-442.
- Curio, E. & Regelman, K. (1985). *The behavioral dynamics of great tits (Parus major) approaching a predator*. *Zeitschr. Tierpsychol.* 69: 3-18.
- Curio, E. (1975). *The functional organization of antipredator behaviour in the Pied Flycatcher: a study of avian visual perception*. *Anim. Behav.* 23: 1-115.
- Curio, E. (1978). *The adaptive significance of avian mobbing. I. Teleonomic hypotheses and predictions*. *Zeitschr. Tierpsychol.* 48: 175-183.

- Curio, E. (1987). *Brood defence in the great tit: the influence of age, number and quality of young*. *Ardea* 75: 35-42.
- Curio, E., Regelmann, K., Zimmermann, U. (1984). *The Defence of First and Second Broods by Great Tit (Parus major) Parents: A Test of Predictive Sociobiol.*. *Z. Tierpsychol.* 66: 101-127.
- Curio, E., Regelmann, K., Zimmermann, U. (1985). *Brood defence in the great tit (Parus major): the influence of life-history and habitat*. *Behav. Ecol. Sociobiol.* 16: 273-283.
- Davies, N. B., Madden, J. R., Butchart, S. H. M. (2004). *Learning fine-tunes a specific response of nestlings to the parental alarm calls of their own species*. *Proc. R. Society B.* 271: 2297-2304.
- de Laet, J. F. (1985). *Dominance and anti-predator behaviour of great tits Parus major: a field study*. *Ibis* 127: 372-377.
- Dominey, W. J. (1983). *Mobbing in colonially nesting fish, especially the bluegill, Lepomis macrochirus*. *Copeia* 4: 1063-1088.
- Donaldson, T. J. (1984). *Mobbing behavior by Stegastes albifasciatus (Pomacentridae), a territorial mosaic damselfish*. *Jap. J. Ichthyol.* 31: 345-348.
- Dugatkin, L. A. & Godin, J.-G. J. (1992). *Predator inspection, shoaling and foraging under predation hazard in the Trinidadian guppy, Poecilia reticulata*. *Environ. Biol. Fish.* 34: 256-276.
- Dugatkin, L. A. (1991). *Dynamics of the tit for tat strategy during predator inspection in the guppy (Poecilia reticulata)*. *Behav. Ecol. Sociobiol.* 29: 127-132.
- Dugatkin, L. A. (1996). *Tit for Tat, by-product mutualism and predator inspection: a reply to Connor*. *Anim. Behav.* 51: 455-457.
- Eberle, M. & Kappeler, P. M. (2006). *Family insurance: kin selection and cooperative breeding in a solitary primate (Microcebus murinus)*. *Behav. Ecol. Sociobiol.* 60: 582-588.
- Eberle, M. & Kappeler, P. M. (2008). *Mutualism, Reciprocity, or Kin Selection? Cooperative Rescue of a Conspecific From a Boa in a Nocturnal Solitary Forager the Gray Mouse Lemur*. *Am. J. Primatology* 70: 410-414.
- Endler, J. A. (1991). *Interactions between predator and prey*. In: Krebs, J. R. & Davies, N. B. (eds.), *Behavioural ecology*. 3 ed.: 169-196. Blackwell Scientific Publications, Oxford.
- Endler, J. A. (1992). *Signals, signal conditions, and the direction of evolution*. *Am. Naturalist* 139: 125-153.
- Erpino, M. J. (1968). *Nest-related activities of Black-billed Magpies*. *Condor* 70: 154-165.
- Eshel, I., Samuelson, L., Shaked, A. (1998). *Altruists, egoists, and hooligans in a local interaction model*. *Am. Econ. Rev.* 88: 157-179.
- Field, J., Shreeves, G., Sumner, S. (1999). *Group size, queuing and helping decisions in facultatively eusocial hover wasps*. *Behav. Ecol. Sociobiol.* 45: 378-385.

- Fischhoff, I. R., Sundaresan, S. R., Cordingley, J., Larkin, H. M., Sellier, M-J., Rubenstein, D. I. (2007). *Social relationships and reproductive state influence leadership roles in movements of plains zebra, Equus burchellii*. Anim. Behav. 73: 825-831.
- Fisher, R. J., Poulin, R. G., Todd, L. D., Brigham, R. M. (2004). *Nest stage, wind speed, and air temperature affect the nest defence behaviours of burrowing owls*. Can. J. Zool. 82: 707-713.
- Forstmeier, W. & Schielzeth, H. (2011). *Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse*. Behav Ecol Sociobiol. Vol. 65, No. 1: 47-55.
- Foster, S. & Ploch, S. (1990). *Determinants of variation in antipredator behavior of territorial male threespine stickleback in the wild*. Ethology 84: 281-294.
- Francis, A. M., Hailman, J. P., Woolfenden, G. E. (1989). *Mobbing by Florida scrub jays: behaviour, sexual asymmetry, role of helpers and ontogeny*. Anim. Behav. 38: 795-816.
- Fridolfsson, A. K. & Ellegren, H. (1999). *A simple and universal method for molecular sexing of non-ratite birds*. J. Avian Biol. 30:116-121.
- Getty, T. (1987). *Dear enemies and the Prisoner's Dilemma: why should territorial neighbors form defensive coalitions?* Am. Zool. 27: 327-336.
- Gill, S. A. & Sealy, S. G. (1996). *Nest defence by yellow warblers: recognition of a brood parasite and an avian nest predator*. Behaviour 133: 263-282.
- Gochfeld, M. (1984). *Antipredator behavior: aggressive and distraction displays of shorebirds*. In: Burger J, Olla BL (eds) Shorebirds: breeding behavior and populations. Plenum Publ. Corp., New York, p. 289-377.
- Godard, R. (1993). *Tit for tat among neighboring hooded warblers*. Behav. Ecol. Sociobiol. 33: 45-50.
- Godin, J-G. J., Classon, L. J., Abrahams, M. V. (1988). *Group vigilance and shoal size in a small characin fish*. Behaviour 104: 29-40.
- Gotceitas, V. & Godin, J-G. J. (1991). *Foraging under the risk of predation in juvenile Atlantic salmon (Salmo salar L.): effects of social status and hunger*. Behav. Ecol. Sociobiol. 29: 255-261.
- Graw, B. & Manser, M. B. (2007). *The function of mobbing in cooperative meerkats*. Anim. behavior. vol. 74, No. 3: 507-517.
- Greig-Smith, P. W. (1980). *Parental investment in nest defense by Stonechats (Saxicola torquata)*. Anim. Behav. 28: 604-619.
- Griffin, A. S. & West, S. A. (2002). *Kin selection: fact and fiction*. Trends Ecol. Evol. 17: 15-21.
- Hamilton, W. D. (1964). *The genetical evolution of social behavior. Part I*. J. Theor. Biol. 7: 1-16.
- Hamilton, W. D. (1971). *Geometry for the selfish herd*. J. Theoretical Biol. 31: 295-311.

- Helfman, G. S. (1989). *Threat-sensitive predator avoidance in damselfish-trumpetfish interactions*. Behav. Ecol. Sociobiol. 24: 47-58.
- Hogstad, O. (1988). *Social rank and antipredator behaviour of willow tits *Parus montanus* in winter flocks*. Ibis 130: 45-56.
- Hogstad, O. (1993). *Nest Defence and Physical Condition in Fieldfare *Trudus pilaris**. J. Orn. 134: 25-33.
- Hogstad, O. (2005). *Sex-differences in nest defence in Fieldfares *Turdus pilaris* in relation to their size and physical condition*. Ibis 147: 375-380.
- Holmgren, N. & Hedenström, A. (1995). *The scheduling of molt in migratory birds*. Evo. Ecol. 9: 354-368.
- Hoogland, J. L. & Sherman, P. W. (1976). *Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality*. Ecol. Monogr. 46:33-58.
- Hoogland, J. L. (1996). *Why do Gunnison's prairie dogs give anti-predator calls?* Anim. Behav. 51: 871-880.
- Horn, H. S. (1968). *The adaptive significance of colonial nesting in the Brewer's blackbird (*Euphagus cyanocephalus*)*. Ecology 49: 682-694.
- Houston, A. I. & McNamara, J. M. (1987). *Singing to attract a mate: a stochastic dynamic game*. J. Theor. Biol. 129: 57-68.
- Houston, A. I. & McNamara, J. M. (1988). *Fighting for food: a dynamic version of the hawk-dove game*. Evo. Ecol. 2: 51-64.
- Hurd, C. R. (1996). *Interspecific attraction to the mobbing calls of black capped chickadees (*Parus atricapillus*)*. Behav. Ecol. Sociobiol. Vol. 38, No. 4: 287-292.
- Impeken, M. (1976). *Responses of laughing gull chicks (*Larus atricilla*) to parental attraction calls and alarm calls, and effects of prenatal auditory experience on responsiveness to such calls*. Behaviour 56: 250-278.
- Jeschke, J. M. & Tollrian, R. (2007). *Prey swarming: which predators become confused and why?* Anim. Behav. 74: 387-393.
- Johnson, L. S. & Albrecht, D. J. (1993). *Does the cost of polygyny in house wrens include reduced male assistance in defending offspring*. Behav. Ecol. Sociobiol. 33: 131-136.
- Klump, G. M. & Shalter, M. D. (1984). *Acoustic behaviour of birds and mammals in the predator context*. Zeitschr. Tierpsychol. 66: 189-226.
- Koenig, W. D. & Dickinson, J. L. (2004). *Ecology and evolution of cooperative breeding in birds*. Cambridge University Press.
- Koenig, W. D., Stanback, M. T., Hooge, P. N. (1991). *Distress calls of the acorn woodpecker*. Condor 93: 637-643.
- Konovalov, D. A., Manning, C., Henshaw, M. T. (2004). *KINGROUP: a program for pedigree relationship reconstruction and kin group assignments using genetic markers*. Mol. Ecol. Notes 4: 779-782.

- Krams, I., Bērziņa, A., Krama, T. (2009). *Group effect in nest defence behaviour of breeding pied flycatchers, *Ficedula hypoleuca**. Anim. Behav. 77: 513-517.
- Krause, J. & Ruxton, G. D. (2002). *Living in groups*. New York: Oxford University Press.
- Kruuk, H. (1964). *Predators and anti-predator behavior of the Black-headed Gull (*Larus ridibundus* L.)*. Behav. Suppl. 11: 1-129.
- Kruuk, H. (1972). *The spotted hyena. A study of predation and social behavior*. University of Chicago Press, Chicago. 335 pp.
- Kruuk, H. (1976). *The biological function of gulls' attraction towards predators*. Anim. Behav. 24: 146-153.
- Kullberg C, Fransson T, Jakobsson S (1996). *Impaired predator evasion in fat blackcaps (*Sylvia atricapilla*)*. Proc. R. Soc. Lond. B. 263: 1671-1675.
- Kullberg, C. & Lind, J. (2002). *An experimental study of predator recognition in great tit fledglings*. Ethology 108: 429-441.
- Le Vin, A. L., Mable, B. K., Arnold, K. E. (2010). *Kin recognition via phenotype matching in a cooperatively breeding cichlid, *Neolamprologus pulcher**. Anim. Behav. Vol. 79, No. 5: 1109-1114.
- Lemmetyinen, R. (1971). *Nest defence behaviour of Common and Arctic Terns and its effects on the success achieved by predators*. Ornis Fenn 48: 13-24.
- Lima, S. L. & Dill, L. M. (1990). *Behavioral decisions made under the risk of predation: a review and prospectus*. Can. J. Zool. 68: 619-640.
- Lind, J., Fransson, T., Jakobsson, S., Kullberg, C. (1999). *Reduced take-off ability in Robins. (*Erithacus rubecula*) due to migratory fuel load*. Behav. Ecol. Sociobiol. 46:65-70.
- Loughry, W. J. (1987). *The dynamics of snake harassment by black-tailed prairie dogs*. Behaviour 103: 27-48.
- Lucas, J. R. & Howard, R. D. (1995). *On alternative reproductive tactics in anurans: dynamic games with density and frequency dependence*. Am. Nat. 146: 365-397.
- Magrath, R. D., Platzen, D., Kondo, J. (2006). *From nestling calls to fledgling silence: adaptive timing of change in response to aerial alarm calls*. Proc. R. Society B. 273: 2335-2341.
- Magurran, A. E. & Pitcher, T. J. (1987). *Provenance, shoal size and the Sociobiol. of predator evasion behaviour in minnow shoals*. Proc. R. Soc. Lond. B 229: 439-465.
- Maklakov, A. A. (2002). *Snake-directed mobbing in a cooperative breeder: anti-predator behaviour or self-advertisement for the formation of dispersal coalitions?* Behav. Ecol. Sociobiol. 53: 372-378.
- Martin, K. & Horn, A. G. (1993). *Clutch defense by male and female Willow Ptarmigan *Lagopus lagopus**. Ornis Scandinavica 24: 261-266.
- Masters, W. M. & Waite, T. A. (1990). *Tit-for-tat during predator inspection, or shoaling?* Anim. Behav. 39: 603-604.

- McNamara J. M., Houston A. I., Szekely, T., Webb J. N. (2002). *Do parents make independent decisions about desertion?* Anim. Behav. Vol. 64, Part 1: 147-149.
- McNamara, J. M., Webb, J. N., Collins, E. J. (1995). *Dynamic optimization in fluctuating environments*. Proc. R. Soc. Lond. B. Sciences 261: 279-284.
- McNamara, J. M., Wilson, E. M. K., Houston, A. I. (2006). *Is it better to give information, receive it, or be ignorant in a two-player game?* Behav. Ecol. Vol. 17. No. 3: 441-451.
- Merritt, P. G. (1984). *Observer recognition by the Northern Mockingbird*. J. Field Ornithol. 55: 25-253.
- Metcalf, N. B. & Ure, S. E., (1995). *Diurnal variation in flight performance and hence potential predation risk in small birds*. Proc R Soc Lond. B. 261: 395-400.
- Milinski, M. (1987). *Tit for tat in sticklebacks and the evolution of cooperation*. Nature 325: 433-435.
- Milinski, M. (1990). *No alternative to tit-for-tat cooperation in sticklebacks*. Anim. Behav. 39: 989-991.
- Milinski, M. (1996). *By-product mutualism, tit-for-tat reciprocity and cooperative predator inspection: a reply to Connor*. Anim. Behav. 51: 458-461.
- Milinski, M., Luthi, J. H., Egger, R., Parker, G. A. (1997). *Cooperation under predation risk: experiments on costs and benefits*. Proc. R. Soc. Lond. B. 264: 831-837.
- Milinski, M., Pfluger, D., Külling, D., Kettler, R. (1990). *Do sticklebacks cooperate repeatedly in reciprocal pairs?* Behav. Ecol. Sociobiol. 27: 17-21.
- Miller, R. C. (1922). *The significance of the gregarious habit*. Ecology. 3: 122-126.
- Montgomerie, R. D. & Weatherhead, P. J. (1988). *Risks and rewards of nest defence by parental birds*. Q. Rev. Biol. 63: 167-187.
- Morgan, M. J. & Colgan, P. W. (1987). *The effects of predator presence and shoal size on foraging in bluntnose minnows, Pimephales notatus*. Environ. Biol. Fishes 20: 105-111.
- Mundry, R. & Nunn C. L. (2009). *Stepwise model fitting and statistical inference: turning noise into signal pollution*. Am Nat. Vol. 173, No1: 119-123.
- Négrel, D. C., Robertson, J., Kleindorfer, S. (2010). *Nestling presence affects the anti-predator response of adult superb fairy-wrens (Malurus cyaneus)*. Acta ethologica Vol. 13, No. 2: 69-74.
- Neudorf, D. L. & Sealy, S. G. (2002). *Distress calls of birds in a neotropical cloud forest*. Biotropica Vol. 34, No. 1: 118-126.
- Nolen, M. T. & Lucas, J. R. (2009). *Asymmetries in mobbing behaviour and correlated intensity during predator mobbing by nuthatches, chickadees and titmice*. Anim. Behav. 77: 1137-1146.
- Olendorf, R., Getty, T., Scribner, K. (2003). *Cooperative nest defence in red-winged blackbirds: reciprocal altruism, kinship or by-product mutualism?* Proc. Biol. Sci. Vol. 271, No. 1535: 177-189.

- Ostreiher, R. (2003). *Is mobbing altruistic or selfish*. Anim. Behav. 66: 145-149.
- Owings, D. H. & Morton, E. S. (1997). *The role of information in communication: an assessment/management approach*. Perspectives in ethology. Vol. 12. Communication (Eds. Owings, D.H., Beecher, M.D. & Thompson, N.S.). Plenum Press, New York. 359-384.
- Owings, D. H. & Morton, E. S. (1998). *Animal vocal communication: A new approach*. Cambridge University Press.
- Owings, D. H. & Owings, S. C. (1979). *Snake-directed behavior by black-tailed prairie dogs (Cynomys ludovicianus)*. Zeitschr. Tierpsychol. 49: 35-54.
- Owren, M. J. & Rendall, D. (1997). *An affect-conditioning model of nonhuman primate vocal signaling*. Perspectives in ethology, Vol. 12, Communication (Eds. Owings, D. H., Beecher, M. D. & Thompson, N. S.). Plenum Press, New York. 299-342.
- Owren, M. J. & Rendall, D. (2001). *Sound on the rebound: Returning form and function to the forefront in understanding nonhuman primate vocal signaling*. Evo. Anthropol. 10: 58-71.
- Packer, C. (1977). *Reciprocal altruism in Papio anubis*. Nature 265: 441-443.
- Patterson, T. L., Petrinovich, L., James, D. K. (1980). *Reproductive value and appropriateness of response to predators by White-crowned Sparrows*. Behav. Ecol. Sociobiol. 7: 227-231.
- Payne, R. B., Payne, L. L., Rowley, I. (1985). *Splendid wren Malurus splendens response to cuckoos: an experimental test of social organization in a communal bird*. Behaviour 94: 108-127.
- Perrone, M. (1980). *Factors affecting the incidence of distress calls in passerine birds*. Wilson Bull. 92: 404-408.
- Pitcher, T. J., Green, D. A. & Magurran, A. E. (1986): "Dicing with death: predator inspection behaviour in minnow shoals". J. Fish Biol. 28: 439-448.
- Požgayová, M., Procházka, P., Honza, M. (2009). *Sex-specific defence behaviour against brood parasitism in a host with female-only incubation*. Behav. Processes 81: 34-38.
- Pulliam, H. R. (1973). *On the advantages of flocking*. J. Theor. Biol. 38: 419-422.
- Pusey, A. & Wolf, M. (1996). *Inbreeding avoidance in animals*. Trends Ecol. Evol. 11: 201-206.
- Rands, S. A., Pettifor, R.A., Rowcliffe, J.M., Cowlishaw, G. (2004). *State-dependent foraging rules for social animals in selfish herds*. Proc. R. Soc. B. 271: 2613-2620.
- Rands, S. A., Johnstone, R.A. (2006). *Statistical measures for defining an individual's degree of independence within state-dependent dynamic games*. BMC Evol. Biol. 6: 81.
- Rands, S. A., Cowlishaw, G., Pettifor, R.A., Rowcliffe, J.M., Johnstone, R.A. (2008). *The emergence of leaders and followers in foraging pairs when the qualities of individuals differ*. BMC Evol. Biol. 8: 51.
- Redmond, L. J., Murphy, M. T., Sexton, K. (2009). *Parental Investment Theory and Nest Defense by Eastern Kingbirds*. Wilson J. Ornithol. Vol. 121, No. 1: 1-11.

- Regelmann, K. & Curio, E. (1986). *How do great tit (Parus major) pair mates cooperate in brood defence?* Behaviour 97: 10-36.
- Robertson, R. J. & Biermann, G. C. (1979). *Parental investment strategies determined by the expected benefits.* Zeitschr. Tierpsychol. 50: 124-128.
- Rohwer, S., Fretwell, S. D., Tuckfield, R. C. (1976). *Distress Screams as a Measure of Kinship in Birds.* Am. Midland Naturalist Vol. 96, No. 2: 418-430.
- Russel, A. F. & Wright, J. (2009). *Avian mobbing: byproduct mutualism not reciprocal altruism.* Trends in Ecology & Evolution Vol. 24, No. 1: 3-5.
- Ryan, M. J. (1998). *Sexual selection, receiver biases, and the evolution of sex differences.* Science 281: 1999-2003.
- Seyfarth, R. M. & Cheney, D. L. (1988). *Empirical tests of reciprocity theory: problems in assessment.* Ethol. Sociobiol. 9: 181-187.
- Shalter, M. D. (1979). *Responses of nesting passerines to alarm calls.* Ibis 121: 362-368.
- Shields, W. M. (1980). *Ground squirrel alarm calls: nepotism or parental care?* Am. Nar. 116: 599-603.
- Shields, W. M. (1984). *Barn swallow mobbing: self-defence, collateral kin defence, group defence or parental care?* Anim. Behav. 32: 132-148.
- Sih, A. (1987). *Predators and prey lifestyles: an evolutionary and ecological overview.* Kerfoot, W. C. & Sih, A. (eds.), Predation: Direct and indirect impacts on aquatic communities: 203-224. University Press of New England, Hanover, NH.
- Slagsvold, T. (1985). *Mobbing behaviour of the Hooded Crow Corvus corone cornix in relation to age, sex, size, season, temperature and kind of enemy.* Fauna Norvegica (C) 8: 9-17.
- Sordahl, T. A. (2004). *Field evidence of predator discrimination abilities in American Avocets and Black necked Stilts.* J Field Orn. Vol. 75, No. 4: 376-385.
- Stacey, P. B. & Koenig, W. D. (1990). *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behaviour.* Cambridge: Cambridge University Press.
- Taborsky, M. & Limberger, D. (1981). *Helpers in fish.* Behav. Ecol. Sociobiol. 8: 143-145.
- Taborsky, M. (1984). *Broodcare helpers in the cichlid fish Lamprologus brichardi their costs and benefits.* Anim. Behav. 32: 1236-1252.
- Tosh, C. R., Krause, J., Ruxton, G. D. (2009). *Basic features, conjunctive searches, and the confusion effect in predator-prey interactions.* Behav. Ecol. Sociobiol. 63: 473-475.
- Trivers, R. L. (1971). *The evolution of reciprocal altruism.* Q. Rev. Biol. 46: 35-57.
- Trivers, R. L. (1972). *Parental investment and sexual selection.* In: Campbell B (ed) Sexual selection and the descent of man, 1871-1971. Aldine Press, Chicago, p. 136-179.

- Trnka, A. & Prokop, P. (2010). Does Social Mating System Influence Nest Defence Behaviour in Great Reed Warbler (*Acrocephalus arundinaceus*) Males?. *Ethology*, 116: 1075-1083.
- van de Pol, M. & Wright, J. (2009). *A simple method for distinguishing within- versus between-subject effects using mixed models*. *Anim. Behav.* 77: 753-758.
- Venuto, V., Ferraiuolo, V., Bottoni, L., Massa, R. (2001). *Distress call in six species of African Poicephalus parrots*. *Ethol. Ecol. Evol* 13: 49-68.
- Verplancke, G., Le Boulengé, É., Diederich, C. (2010). *Differential foraging in presence of predator and conspecific odors in bank voles: a field enclosure study*. *Ecological Research*. Vol. 25, No. 5: 973-981.
- Wallin, K. (1987). *Defence as parental care in tawny owls (Strix aluco)*. *Behaviour*. 102: 213-230.
- Walther, F. R. (1969). *Flight behaviour and avoidance of predators in Thomson's gazelle (Gazella thomsoni Guenther 1884)*. *Behav.* 34: 184-221.
- Weatherhead, P. J. (1979). *Do Savannah Sparrows commit the Concorde Fallacy?* *Behav. Ecol. Sociobiol.* 5: 373-381.
- Welbergen, J. A. & Davies, N. B. (2008). *Reed warblers discriminate cuckoos from sparrowhawks with graded alarm signals that attract mates and neighbours*. *Anim. Behav.* Vol. 76, 3: 811-822.
- Wilkinson, G. S. (1984). *Reciprocal food sharing in the vampire bat*. *Nature* 308: 181-184.
- Wilson, A. D. M., & Godin, J-G. J. (2010). *Boldness and intermittent locomotion in the bluegill sunfish, Lepomis macrochirus*. *Behav. Ecol.* Vol. 21, No. 1: 57-62.
- Wise, K. K., Conover, M. R., Knowiton, F. F. (1999). *Response of coyotes to avian distress calls: Testing the startle-predator and predator-attraction hypotheses*. *Behav.* 136: 935-949.
- Wright, J., Berg, E., de Kort, S. R., Khazin, V., Maklakov, A. A. (2001a). *Safe Selfish Sentinels in a Cooperative Bird*. *Anim. Ecol.* Vol. 70, No. 6: 1070-1079.
- Wright, J., Berg, E., de Kort, S. R., Khazin, V., Maklakov, A. A. (2001b) *Cooperative sentinel behaviour in the Arabian babbler*. *Anim. Behav.* 62: 973-979.
- Wright, J., Maklakov, A. A., Khazin, V. (2001c). *State-dependent sentinels: an experimental study in the Arabian babbler*. *Proc. R. Soc. Lond. B.* Vol. 268, No. 1469: 821-826.