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Emphasising Theory and
Method: Topics in
Comparative Psychology

Kevin Brewer

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Orsett Psychological Services
PO Box 179
Grays
Essex
RM16 3EW
UK

orsettpsychologicalservices@phonecoop.coop

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Kevin Brewer BSocSc, MSc

An independent academic psychologist, based in England, who has written extensively on different areas of psychology with an emphasis on the critical stance towards traditional ideas.

A complete listing of his writings at <http://kmbpsychology.jottit.com> and <http://psychologywritings.synthasite.com/>.

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1. DEBATING SOCIAL MONOGAMY IN PRIMATES

Social monogamy (or pair-bond) is much rarer in mammals (about 3% of species) than among birds (about 90% of species) (Opie et al 2013a). In the latter case, successful rearing of offspring needs both parents (ie: biparental care), and this is one of the main reasons proposed for the evolution of monogamy. Among New World primates that give birth to twins (eg: callitrichids, like marmosets), for example, monogamy has evolved (Opie et al 2013a).

Another explanation for the evolution of monogamy is as mate-guarding by males against rivals when females are geographically separate (eg: dik-dik; Brotherton and Manser 1997).

A third possibility is protection against infanticide by males. Females when lactating tend not to be receptive to males, so one male may kill the offspring of another male in order to make the mother sexually receptive in a situation of no settled males and females together (van Schaik et al 1990) ¹. Primates have larger brains, which means longer periods of dependency for the young, and thus the risk of infanticide.

The big question is whether there is a hypothesis/general selection pressure that explains the evolution of monogamy in primates as a whole group.

Opie et al (2013a) tested the three hypotheses above for the evolution of social monogamy in primates using data on the evolutionary history of 230 species, and infanticide. Male infanticide preceded the shift of a species to social monogamy, while biparental care evolved after the shift, and mate-guarding seems to contribute to the maintenance of monogamy rather than cause it. Species with low infanticide tend to have polygyny and do not change to monogamy. Opie et al (2013a) added that "socially monogamous species have lower risk of infanticide, in terms of the proportion of the breeding cycle devoted to lactation (the 'weaning proportion'), than do polygynous species. This finding hints at one mechanism by which social monogamy may reduce infanticide risk: social monogamy facilitates a shorter lactation period compared with gestation, thereby reducing infanticide risk" (p13329).

However, Opie et al (2013a) did accept that there are primates with high infanticide (eg: gorillas, langurs) where social monogamy has not evolved. They said: "a switch to social monogamy may only be possible where ecological conditions permit. Other factors play a

¹ There are exceptions - for example, marmosets conceive fourteen days after giving birth to twins, so they are lactating while pregnant (Dixson 2013).

role in determining optimal grouping patterns: predation pressure drives up group size and resource distribution and habitat use also impact on group size and structure. Hanuman langurs and gorillas incur high levels of mortality from infanticide but also live in a habitat with high predation risk. The pressure to maintain cohesive social groups as an anti-predator defence may render social monogamy a non-starter" (p13329).

Other strategies in primates to combat infanticide including polygynandrous mating (eg: female chimpanzees mate with many males in the social group, and males defend all females and infants in their territory) (Opie et al 2013a).

Lukas and Clutton-Brock (2013) analysed data on 330 primate species, and argued that mate-guarding of isolated females was the basis to the evolution of monogamy. In such a situation the male will then provide care for the offspring.

de Waal and Gavrillets (2013) preferred this explanation. They stated that "data on infanticide is notoriously hard to obtain, and when the authors [Opie et al 2013a] restricted their analysis to the subset of studies with the most reliable data, the connection with infanticide fell away" (p15167).

For example, direct observation of infanticide exists in around 6% of all primate species (Dixson 2013)². Due to lack of data, Opie et al (2013a) made the assumption that species with longer periods of lactation (relative to period of gestation) are at greater risk of male infanticide. Dixson (2013) made this criticism: "one problem in comparing this measure across different taxonomic groups of primates is that its evolution may have been influenced by different selective pressures in different lineages. Opie et al may therefore be comparing 'apples with oranges'" (pE4937). Opie et al (2013b) countered this criticism.

Lukas and Clutton-Brock (2014) argued that Opie et al (2013a) "underestimated the frequency of male infanticide by classifying many polygynous species as not showing male infanticide on the basis of insufficient evidence" (pE1674)³. Opie et al (2014) defended their methodology against this criticism.

de Waal and Gavrillets (2013) questioned the

² Infanticide has been used to explain the evolution of many different behaviours (eg: female sexual skin swellings; multiple partner matings) (appendix 1A), but there is insufficient data (Dixson 2013).

³ Opie et al (2013a) classified species with less than twenty scientific studies showing infanticide as insufficient data. Many of the studies were medical reports of captive animals where "experimental conditions limit any possibility of male infanticide" (Lukas and Clutton-Brock 2014).

application of findings to humans, and suggested that monogamy "did not evolve in the genetic sense at all, but rather in a cultural sense" (p15168).

APPENDIX 1A - THREAT OF INFANTICIDE AND CO-OPERATION

Co-operation among social animals can take different forms. One way is suppression of reproduction - ie: a limited number of individuals or one individual reproduces and others help in the upbringing. Because all members of the group are genetically related, the non-breeding helpers maximise their inclusive fitness by maximising the fitness of the group (ie: survival of the offspring).

But the suppression of reproduction has to be policed. For example, among social insects, eggs laid by females other than the queen are destroyed (ie: infanticide) (eg: Ratnieks and Visscher 1989). In some species of insect, this leads to the evolution of female workers who cannot reproduce or almost cannot (Cant et al 2014).

Another evolutionary response to infanticide is synchronised breeding (females giving birth on same day), which Cant et al (2014) found in their seven-year field experiment with wild banded mongooses (*Mungos mungo*) (figure 1.1) in Uganda. These animals live in mixed-sex groups of about twenty adults (and offspring). At each of the four breeding times per year, the majority of the offspring are from the dominant females with some from subordinate females. Offspring care is communal.



(Source: JP)

Figure 1.1 - Banded mongoose.

In three experiments, Cant et al (2014) created asynchronous birth (ie: different females giving birth on different days) by injecting some females with a contraceptive. When the contraceptive was given to the dominant females, and only the subordinate females gave birth, litter failure (ie: death of newborns) was significantly higher than normal. This suggested that "dominant females kill communal litters that are certain not to contain their own young, and hence that subordinates can evade infanticide by synchronising birth to the same day as dominants. In contrast, suppression of subordinate females did not trigger whole-litter infanticide in the first week after birth" (Cant et al 2014 p328). The infanticide only occurred for early-born offspring (ie: before dominant females) not late-born.

REFERENCES

- Brotherton, P.N.M & Manser, M.B (1997) Female dispersion and the evolution of monogamy in the dik-dik Animal Behaviour 54, 6, 1413-1423
- Cant, M et al (2014) Policing of reproduction by hidden threats in a co-operative mammal Proceedings of the National Academy of Sciences, USA 111, 1, 326-330
- de Waal, F.B.M & Gavrillets, S (2013) Monogamy with a purpose Proceedings of the National Academy of Sciences, USA 110, 38, 15167-15168
- Dixon, A.F (2013) Male infanticide and primate monogamy Proceedings of the National Academy of Sciences, USA 110, 51, E4937
- Lukas, D & Clutton-Brock, T.H (2013) The evolution of social monogamy in mammals Science 341, 526-540
- Lukas, D & Clutton-Brock, T.H (2014) Evolution of social monogamy in primates is not consistently associated with male infanticide Proceedings of the National Academy of Sciences, USA 111, 17, E1674
- Opie, C et al (2013a) Male infanticide leads to social monogamy in primates Proceedings of the National Academy of Sciences, USA 110, 33, 13328-13332
- Opie, C et al (2013b) Reply to Dixon: Infanticide triggers primate monogamy Proceedings of the National Academy of Sciences, USA 110, 51, E4938
- Opie, C et al (2014) Reply to Lukas and Clutton-Brock: Infanticide still drives primate monogamy Proceedings of the National Academy of Sciences, USA 111, 17, E1675
- Ratnieks, F.L.W & Visscher, K.P (1989) Worker policing in the honeybee Nature 342, 796-797
- van Schaik, C.P et al (1990) The evolution of monogamy in large primates: A new hypothesis and some crucial tests Behaviour 115, 1-2, 30-61

2. VISUAL DECEPTION

2.1. MASQUERADE

Masquerade is an anti-predator strategy that the involves the animal closely resembling an inedible object, like a twig, a stone, or bird droppings (table 2.1). It is different to camouflage, where the aim is to avoid detection, because it "appears to be an adaptation that reduces the risk of predation by causing predators to misclassify prey as a specific model object" (Suzuki and Sakurai 2015 p79).

- Stone - round-tailed horned lizard (*Phrynosoma modestum*) flatten their bodies to look like stones.
- Twig - twig-mimicking caterpillars stay rigid to enhance their resemblance to twigs.
- Bird droppings - caterpillars of some moths bend their bodies as they rest on branches or leaves to look like bird droppings.

(Source: Suzuki and Sakurai 2015)

Table 2.1 - Examples of masquerade.

Masquerading prey match the objects in size often, live in habitats where the objects are expected, and adopt specific postures to increase their resemblance to the model objects (Suzuki and Sakurai 2015) ⁴.

Suzuki and Sakurai (2015) found that the bent posture is a deliberate and beneficial strategy in their experiment. They created four types of artificial caterpillars of the *Macrauzata maxima* moth from pastry - (i) bird dropping colour (white and black) and bent, (ii) bird dropping colour and straight, (iii) green colour and bent, and (iv) green colour and straight.

The artificial caterpillars were left in 22-24 cherry trees at each of nine sites in Tokyo, Japan. The final sample was 404. Survival was measured by the caterpillar being present seven hours later and having no

⁴ Imperfect or partial mimicry may be a successful prey defence as well because of "overshadowing" (MacKintosh 1976). Partial mimicry is where a palatable prey copies one aspect of the unpalatable prey (eg: same colour), but not the other (eg: different shape).

In an experimental context, Kazemi et al (2014) taught wild blue tits to discriminate between symbols (based on colour, shape and pattern) that signalled rewarding prey and non-rewarding prey. The birds, however, subsequently avoided novel prey with symbols of the same colour as non-rewarding prey, but not the same shape or pattern. This showed that "high-salience discriminatory traits (in this case colour) can overshadow other informative traits, allowing incipient mimics a significant survival advantage even if they share only one trait with the model" (Sherratt et al 2015 p74).

visible peck marks. The main predators are Japanese tits, grey starlings, and tree sparrows. It was found that bird dropping colour and bent artificial caterpillars had a significantly better survival rate (90%) than bird dropping colour and straight (less than 75%) and the green colour caterpillars (both around 80%).

Suzuki and Sakurai (2015) observed: "Bent posture may have evolved in long and slender caterpillars with bird dropping coloration, because their body shape would be very different from real bird droppings when they were elongated... In these species, a bent posture may allow caterpillars to retain the benefits of masquerading, even when their body length exceeds the natural size of bird droppings" (p82).

2.2. VISUAL LURE

Colour is a key aspect of visual communication. It can also be used in deceptive signalling (eg: colour-based prey lures used by predators). These lures include food or reproductive signals that attract the prey. The sensory trap model (Christy 1995) explains the lures as "signals thought to exploit receiver biases" (White and Kemp 2015).

For example, female guppies (*Poecilia reticulata*) show a strong preference for small orange-coloured stimuli, which resemble a male sexual signal, and their predator, a prawn (*Macrobrachium crenulatum*) has evolved orange pincer spots.

Tso et al (2007) showed that bright colouration was a lure used by the orchid spider (*Leucauge magnifica*) in Taiwan. Eight female spiders were video recorded for six days, and the number of prey for different times of the 24-hour period were calculated. The peak hunting time was found to be between 7 pm and 1 am.

Then the researchers manipulated the body colour of some of the spiders with paint. The control spiders intercepted three times as many moths per hour per 100 cm² of orb area as the painted spiders.

The results showed that this spider is a nocturnal hunter, and that it uses its bright body colouration as a visual lure during this time ⁵. Its moth prey is able to detect bright colours in dim light and use that to find food. The yellow stripes on the spider's abdomen is assumed to resemble a flower food source to the moth ^{6 7}.

⁵ Usually spiders that hunt at night use olfactory cues to lure their prey - eg: bolus spider mimics the sex pheromone of the moth (Tso et al 2007).

⁶ Similar nocturnal visual lure has been reported in the giant wood spider (*Nephila pilipis*) (Chuang et al 2007), for instance.

⁷ Other painting experiments have shown the importance of bright body colouration as a visual lure

But the yellow stripes on the ventrum of the spider are not very large. Tso et al (2007) wondered why: "There may be two reasons for such small visual lures. First, although the bright yellow body colouration of orchid spiders is attractive to nocturnal insects, if the whole body is covered by such colouration, the contour of the spider will be more obvious to insects. Prey will quickly learn to associate the colour with danger by recognising the shape of the images. Second, the size of the ventrum stripes might be constrained by strong predation pressure. The major predators of orb-weaving spiders are dipteran or hymenopteran parasitoids... most of which are visually oriented diurnal predators. A large area of bright coloration on the spiders' body will make it easily detected by those predators. Therefore, the size of orchid spiders' yellow ventrum stripes seems to be a product of various counteracting selection pressures involved in spider-prey insect and spider-predatory insect visual interactions" (p792).

Body colouration may fulfil more than one function. Lin et al (2015) found that the white stripe on male nocturnal fishing spiders (*Dolomedes raptor*) attracted females, and prey.

In the latter case, dummy spiders (with or without a white stripe) were left in a forest area in Taiwan. The number of prey approaching per hour was calculated from six hundred hours of video recordings. The dummies with white stripes attracted significantly more prey (0.4 vs 0.1 per hour).

The researchers investigated the role of the stripes in mate attraction by categorising natural variation among males. A link was found to body size and weight, which suggested that the white stripe area signalled these characteristics to females.

Thirty-one males were then fed a high or low nutrition diet, and it was found that the former had larger white stripe areas. This confirmed the role of the stripe area as a honest signal of health.

Next females were offered a male whose stripe had been painted brown or a unpainted male, and they preferred the latter (85% vs 40% of trials).

REFERENCES

- Chuang, C.Y et al (2007) Diurnal and nocturnal prey luring of a colourful predator Journal of Experimental Biology 210, 3830-3837
- Christy, J.H (1995) Mimicry, mate choice, and the sensory trap hypothesis American Naturalist 146, 171-181
- Hauber, M.E (2002) Conspicuous colouration attracts prey to a stationary predator Ecological Entomology 27, 686-691
- Kazemi, B et al (2014) Stimulus salience as an explanation for imperfect mimicry Current Biology 24, 965-969
- Lin, T-S et al (2015) A dual function of white colouration in a nocturnal spider *Dolomedes raptor* (Araneae: Pisauridae) Animal Behaviour 108, 25-32
- Mackintosh, N.J (1976) Overshadowing and stimulus intensity Animal Learning and Behaviour 4, 186-192
- Sherratt, T.N et al (2015) Hierarchical overshadowing of stimuli and its role in mimicry evolution Animal Behaviour 108, 73-79
- Suzuki, T.N & Sakurai, R (2015) Bent posture improves the protection value of bird dropping masquerading by caterpillars Animal Behaviour 105, 79-84
- Tso, I-M et al (2007) Nocturnal hunting of a brightly coloured sit-and-wait predator Animal Behaviour 74, 787-793
- White, T.E & Kemp, D.J (2015) Technicolour deceit: A sensory basis for the study of colour-based lures Animal Behaviour 105, 231-243

3. BROOD PARASITE AND HOST MANIPULATION

Parasites depend on hosts to transmit themselves, and they are able to manipulate hosts to increase successful transmission. For example, *Toxoplasma gondii* (a protozoan) can live in rats, but has a definitive host of cats (where it is able to sexually reproduce). It is able to manipulate the rodent host by making the rat less "fearful" of cats, and thus more likely to be killed and eaten (ie: successful transmission) (Berdoy et al 2000). Changing the host's behaviour like this can be classed as an adaptive extended phenotype of the parasite (Dawkins 1982).

Brood-parasite birds (eg: cowbirds, cuckoos) lay their eggs in the nests of other species (hosts) who provide the parental care for their young. But how do these birds manipulate the host's behaviour?

One way is to attack nests⁸ and destroy eggs/nestlings of the potential host when it is too late to parasitise them. The parasite needs to put their egg in the nest soon after the host has laid (ie: early in the incubation period). Destroying nests is a way to manipulate hosts into starting a new reproductive cycle, and thus offering the opportunity for parasitism⁹. This is known as the "farming hypothesis" (Arcese et al 1992).

This hypothesis requires that the parasite is able to tell the stage of the host's reproductive cycle in terms of the egg development. Swan et al (2015) investigated this in the brown-headed cowbird (*Molothrus ater*) (figure 3.1) in laboratory experiments and with observational data.

Forty females captured¹⁰ in Ontario, Canada were used in the "cafeteria style" choice experiments (ie: two nests at either end of a cage). Three types of experiments were performed in which each trial lasted twenty minutes or until a nest was attacked.

1. Direct method: developmental stage - There was a nest choice of red-winged blackbird (*Agelaius phoeniceus*) eggs laid one day or over ten days ago (three in each nest). In seventeen trials where attacks occurred, late-stage nests were attacked by the cowbirds significantly more often than the early-stage nests.

2. Indirect method: egg number - There was a nest choice

⁸ Including puncture eggs, remove eggs to cause host to abandon nest, or occasionally consume eggs (Swan et al 2015).

⁹ Cowbirds also attack the eggs of the host to increase the chances of their egg (incubation efficiency hypothesis), to reduce future competition in the nest for their offspring (competition reduction hypothesis), or as revenge if their egg is rejected (mafia hypothesis; appendix 3A) (Swan et al 2015).

¹⁰ The capture of animals can have lasting effects (appendix 3B).



(Source: DickDaniels <http://carolinabirds.org/>)

Figure 3.1 - Female brown-headed cowbird.

of four or two unfertilised eggs of the yellow canary (*Serinus flaviventris*). Eighteen trials involved attacks, and significantly more attacks were on the four-egg nests.

3. Indirect method: changing number of eggs - Using plasticine eggs, cowbirds were shown a nest containing four eggs over three consecutive days, and a nest with two eggs on the first day which became three eggs on the second day, and four eggs the next day. Then the cowbirds were free to attack the nests. There was no difference between the nests in number of attacks.

The observational data came from video recordings of song sparrow (*Melospiza melodia*) nests near Victoria, British Columbia over ten years. Attacks on non-parasitised nests significantly positively correlated with time (ie: later in the egg development cycle), but there was no relationship for parasitised nests.

The findings from Swan et al's (2015) experiments and observations showed that cowbirds are able to tell the stage of the reproductive cycle of their potential hosts based on egg development (determined by puncturing

the egg) (experiment 1), and by absolute clutch size (ie: less eggs is a sign of early in incubation cycle) (experiment 2). The first is a direct method of assessing host egg stage, and the second is indirect.

However, the cowbirds did not use the indirect method in experiment 3 of watching eggs added to the clutch each day. This is not because cowbirds do not monitor their hosts' nests over multiple days before parasitism (appendix 3C). White et al (2009) had got contrary results here (appendix 3D).

APPENDIX 3A - "MAFIA BEHAVIOUR"

Hoover and Robinson (2007) removed cowbird eggs from some prothonotary warbler (*Protonotaria citrea*) nest-boxes in a field experiment over four years in southern Illinois, USA. There were five conditions in the experiment with a total of 182 nests/nest-boxes (table 3.1). It was found that 56% of "ejector" nests (ie: where cowbird egg removed by experimenters) were attacked by cowbirds compared to 6% of "acceptor" nests (where egg not removed). This is taken as evidence of retaliation by the cowbirds against the removal of their eggs^{11 12}.

- 1 - Ejector - cowbird egg removed by researchers on day put there. Attacks on these nests by cowbirds would support the "mafia hypothesis".
- 2 - Non-parasitised nests - attacks on these nests would support the "farming hypothesis".
- 3 - Acceptors - parasitised nests.
- 4 - Ejector/access denied - as condition 1, but access to the nest was denied to cowbirds by making the entrance too small after removal of their egg. This was to check that damage to the nests was due to cowbirds and not other birds.
- 5 - As condition 2 but access denied - control as in condition 4.

Table 3.1 - Five conditions in experiment by Hoover and Robinson (2007).

There was also evidence to support the "farming hypothesis" as 20% of non-parasitised nests were

¹¹ Hoover and Robinson (2007) pointed out: "Unlike farming, mafia behaviour in a brood parasite can slow the evolution of ejection behaviour in hosts. Retaliation may also mediate a change in rejection behaviour of individual hosts, resulting in those individuals being more likely to accept subsequent parasitism" (p4481).

¹² An interesting observation was that hosts produced more offspring in parasitised than non-parasitised nests (3 vs 1) (Hoover and Robinson 2007).

attacked. The researchers also found that the "re-nests" were significantly more frequently parasitised (85%) than all nests (overall parasitised rate 36%).

APPENDIX 3B - CAPTURE, HANDLING, MARKING AND SAMPLING (CHMS)

The marking of an animal is common in research, or more correctly, capture, handling, marking and sampling (CHMS) (Schlicht and Kempenaers 2015). Concentrating on birds and CHMS, studies have investigated the long-term effects on reproduction (eg: nest desertion, brood size), survival, physical condition, and behaviour (eg: migration, foraging) as well as the immediate physiological effects of CHMS. Schlicht and Kempenaers (2015) observed that "most researchers are well aware that birds perceive CHMS as a stressful event..., but in general regard them as being able to cope well with CHMS and recover quickly returning to normal behaviour" (pp63-64).

Schlicht and Kempenaers (2015) concentrated on the effects of CHMS on blue tit (*Cyanistes caeruleus*) parents in a population in south Germany. An adult bird was taken from the nestbox when the chicks were 9-11 days old (captured), carried in a bird bag to the researchers' van, handled, measured, sampled (eg: blood), and released back to their territory. A total of 255 individuals were taken away from their territories for an average of thirty minutes during the breeding seasons of 2010-2012.

The speed of the return of the bird to their nest was measured, with the average being 4.2 hours. "These absence durations are much longer than those observed after a simple disturbance at the nest (checking the nest during the nestling period). This result highlights that CHMS disturbances may alter immediate behaviour of individuals for a substantially longer period than is generally assumed" (Schlicht and Kempenaers 2015 p69). But once returned, the birds quickly resumed "parental duties in a normal fashion".

Schlicht and Kempenaers (2015) stated: "Birds may perceive capture as a predation event... and react by avoiding the location of capture (the nest), returning only after they have assessed the predation risk to be reduced again to before-capture levels. This could explain why normal visiting patterns re-emerge, once parents have returned" (p70).

APPENDIX 3C - FEMALE COWBIRD MEMORY

Female cowbirds have a larger hippocampus and consequently better memory than males (Guigueno et al

2014). This would make sense as female search, find and revisit host nests, and need to remember their location and number of eggs present.

This sex difference fits with the adaptive specialisation hypothesis (Sherry 2006), which states that brains are adaptively specialised to solve survival-related problems.

Guigueno et al (2014) tested whether the sex difference in cowbird memory was seasonal only (ie: during the breeding season). A delayed-matching-to-sample spatial memory task was used with seven females and seven males tested individually. Initially, the bird was let into an enclosure with twenty-five cups, of which only one contained food. They were left to find the food (learning phase). Either one hour or twenty-four hours later, they were returned to the enclosure. The food was in the same cup (test phase). A score was made of number of errors before finding food, and path length between the first cup uncovered and the food-laden (baited) cup. The experiment was performed during breeding and non-breeding conditions (which were artificially induced).

Females made fewer errors and had a more direct path than males irrelevant of breeding or non-breeding conditions, and with both retention intervals. The sex difference in memory appears not to be seasonal, though the researchers cautioned that the birds were captive - "because captivity may differentially affect the hippocampus, we cannot preclude the existence of seasonal differences in free-living birds" (p3).

They also admitted: "Although our spatial memory task did not specifically test memory for host nests, our task likely tested for common underlying cognitive mechanisms which tap into the abilities that females use to re-visit host nests" (Guigueno et al 2014 p4).

APPENDIX 3D - WHITE ET AL (2009) AND NUMBER SENSE

Cowbirds lay one per day just before sunrise in different nests of over 200 host bird species. The egg laying needs to be synchronised with host incubation readiness (which can range from eleven to sixteen days), and it occurs in nests (containing two to eight eggs). "Consequently, the ability to remember the number of host-eggs present in nests and changes in host-egg number between past and present visits is likely to be selectively advantageous" (Low et al 2009 p775).

White et al (2009) presented female cowbirds with a three-egg nest (Nest 1A) and a one-egg nest (Nest B) initially. Then the birds watched as one egg was added daily for three days to Nest A (ie: 3 becomes 6), and two eggs were added to Nest B (ie: 1 becomes 3). The former

simulated a host still laying, while the latter simulated a host that had begun incubating. When given access to the nests, the cowbirds spent more time around Nest A. Is this evidence of basic number sense (counting) or use of sensory cues like greater visual and tactile area of six eggs?

White et al (2009) performed another experiment with three nests. Nest AA started with one egg, and had another added the next day and the next day (total three), while Nest BB started with two eggs and had another added the next day only. Nest CC had three eggs throughout the experiment.

At the beginning of the experiment (Day 1), given the choice, cowbirds preferred Nest CC. On Day 2 they preferred nests that had changed (ie: BB and CC). On Day 3 faced with three equal nests, they preferred Nest AA - "that changed in egg-number in accordance with the number of days that had elapsed from their initial visit. Therefore, cowbirds appeared to remember changes in egg-number between visits and spent longer periods investigating nests with the correct accumulated number of eggs in relation to elapsed days" (Low et al 2009 p775).

Saying that, Low et al (2009) were cautious about attributing number sense - "it is not yet clear why birds would need to develop numerical skills in the first place" (p776).

REFERENCES

- Arcese, P et al (1992) Stability, regulation, and the determination of abundance in an insular song sparrow population Ecology 73, 805-822
- Berdoy, M et al (2000) Fatal attraction in rats infected with *Toxoplasma gondii* Proceedings of the Royal Society B: Biological Sciences 267, 1591-1594
- Dawkins, R (1982) The Extended Phenotype Oxford: OUP
- Guigueno, M.F et al (2014) Female cowbirds have more accurate spatial memory than males Biology Letters 10: 20140026
- Hoover, J.P & Robinson, S.K (2007) Retaliatory mafia behaviour by a parasitic cowbird favours host acceptance of parasitic eggs Proceedings of the National Academy of Sciences, USA 104, 11, 4479-4483
- Low, J et al (2009) Wild number sense in brood parasite Brown-headed Cowbirds Ibis 151, 775-777
- Schlicht, E & Kempenaers, B (2015) Immediate effects of capture on nest visits of breeding blue tits, *Cyanistes caeruleus*, are substantial Animal Behaviour 105, 63-78
- Sherry, D.F (2006) Neuroecology Annual Review of Psychology 57,167-193
- Swann, D.C et al (2015) Brood parasites manipulate their hosts: Experimental evidence for the farming hypothesis Animal Behaviour 105,29-35
- White, D.J et al (2009) Counting chicks before they hatch: Female cowbirds can time readiness of a host nest for parasitism Psychological Science 20, 1140-1145

4. MATERNAL INVESTMENT AND BEHAVIOUR

4.1. FEMALE INVESTMENT

Female birds can vary their investment in their eggs - for example, the size of the egg, which influences size of offspring, growth rate, and chances of survival (particularly in the early days post-hatching). This maternal investment is independent of male investment, but is influenced by the attractiveness of the male. For example, female mallards mated with attractive males laid larger eggs than females with less attractive mates, while zebra finches produced eggs containing more testosterone ¹³ (Bonato et al 2009a).

The issue is then what do females find attractive (ie: what sexually dimorphic characteristics to discriminate between males), and this varies with species. For example, Bonato et al (2009a) found that among ostriches (*Struthio camelus*) (figure 4.1) it was colour of the neck, white and black body feathers, and brightness of black feathers (but not bill and legs). These are all exposed to the female during the courtship display ("kantling" behaviour), where the male sits on his legs with wings held forward, and swings his neck from side to side (Bonato et al 2009a).



(Source: KuK; in public domain)

Figure 4.1 - Ostriches in South Africa.

¹³ The level of testosterone has been shown to influence the intensity of begging of hatchlings, and consequently, the rate of growth (Bonato et al 2009a).

Bonato et al (2009a) studied two breeding flocks of South African black ostriches at an experimental farm in Oudtshoorn, South Africa (figure 4.2) in 2005-6.



(Drawn with MapCreator 2.0)

Figure 4.2 - Location of Oudtshoorn.

The ostrich has a communal nesting system where many females lay in the same nest of a territorial male, but care is provided by the major male and major female only. Major females, however, also lay in other territorial males' communal nests (ie: they are minor females here) (Kimwele and Graves 2003). "Therefore, females usually mate preferentially with one specific male on his territory, and then with neighbouring males at a lower rate" (Bonato et al 2009a p1030).

Particular aspects of appearance like exaggerated ornamentation in males is a signal of quality of genes to females. Ornaments signal good general condition of the individual, high ability in finding food to grow such features, or the ability to fight off parasites (appendix 4A). In birds, length of tail feathers, plumage colouration, and beak colouration are relevant signals (Bonato et al 2009b).

The ability to fight off parasites and disease is known as immunocompetence. Bonato et al (2009b)

experimentally tested the immunocompetence of fifteen South African black ostrich males by inoculating them with two vaccines. The number of anti-bodies produced in the following month was the measure of immunocompetence.

Leg, feather, and bill colouration preferred by females were associated with more anti-bodies. The differences in colouration of these three parts of the body are honest signals¹⁴ of the immunocompetence of the male ostriches.

4.2. CURRENT AND FUTURE INVESTMENT

Species that reproduce more than once in a lifetime have to balance their investment in the current offspring and the future opportunity for reproduction and offspring. The balance is known as the breeding effort threshold, and it varies depending on environmental costs and the physiological state of the individual (Gonzalez-Medina et al 2015).

Experiments with sea-birds that manipulate the demands of the offspring showed that (Gonzalez-Medina et al 2015):

a) Some parents adjust their effort in response (offspring's demands fully met) - eg: blue-footed booby (Gonzalez-Medina et al 2015);

b) There is a partial adjustment by some parents (ie: offspring's demands not met) - eg: laughing gull (Gonzalez-Medina et al 2010);

c) Some parents do not adjust - eg: Manx shearwater (Hamer et al 1998).

Previous research with boobies (eg: Velando and Alfonso-Alvarez 2003) had found that there was a sex difference in response to increasing demands of offspring, with males monitoring their own body mass at the expense of offspring (partial adjustment), while females increased their investment in the current offspring at the expense of their own body mass.

Manipulating the demands of the offspring can be done through supplementary feeding or through cross-fostering experiments. For example, in the latter case, Gonzalez-Medina et al (2015) swapped the broods of blue-footed booby (*Sula nebouxii*) (figure 4.3) parents at a nesting site on the Isla El Rancho, Sinaloa, Mexico

¹⁴ Honest signals of male quality are crucial for females (appendix 4B).



(Source: Hans Stieglitz)

Figure 4.3 - Blue-footed boobies.

(figure 4.4). Both parents provision the nest for about six months.



(Drawn with MapCreator 2.0)

Figure 4.4 - Location of Isla El Rancho.

There were four experimental conditions:

1. Increased demands - One-week olds replaced by two-week olds (n = 13 broods).
2. Reduced demands - Two-week olds replaced by one-week olds (n = 13).
3. Control for increased demands - One-week olds exchanged for other one-week olds (n = 6).
4. Control for reduced demands - Two-week olds exchanged for same age (n = 7).

The foraging effort (ie: number of trips) and time spent at the nest were calculated for periods of continuous monitoring.

Increased demands from the offspring (condition 1) led to more foraging trips and less time at the nest compared to the control (condition 3), with no sex difference. Gonzalez-Medina et al (2015) noted that "the parents with increased demands showed muscular damage as a result of the increase in foraging effort" (p14).

In condition 2 (reduced demands), the only difference was that females spent less time at the nest compared to males and to the control (condition 4). Gonzalez-Medina et al (2015) urged caution, though, with this finding: "This intriguing result is difficult to explain considering brood demands. In the context of brood value, females may decrease attention to their new brood because they regard their brood to be of lower reproductive value (ie: smaller chicks might have a lower chance of survival, or females might perceive that their feeding of chicks is not reflected in chick growth and therefore regard them as sick or undernourished with a low chance of survival)" (p14).

Overall, "the ability of adults to adjust breeding effort (within certain limits) can buffer the needs of their offspring across different scenarios throughout the breeding season, but it has short-term physiological costs and may also be related to long-term survival" (Gonzalez-Medina et al 2015 p14).

4.3. MOTHER-OFFSPRING RECOGNITION

Parent-offspring recognition involves visual and olfactory cues when nearby, and vocal cues further away. This latter type of recognition is more important in large groups, where parent-offspring separation is common, and/or the offspring are mobile. For example, among otariids ("eared seals"), mothers leave their pups on land during the lactation period (between 4-18 months)

to forage at sea. Vocal recognition is well developed here as the returning mother seeks to find her pup¹⁵. But among phocids ("earless seals"), where females stay with the pup for lactation of only 4-60 days, vocal recognition is limited (ie: absent or unidirectional) (Sauvé et al 2015).

The harbour seal (*Phoca vitulina*) is one of the exceptions among phocids (table 4.1). The mothers perform short foraging trips at sea, and the pups are mobile during the 21-42 day period of lactation. "These traits imply greater selection pressures for an effective mother-pup vocal recognition system in harbour seals compared to most phocids" (Sauvé et al 2015 p110).

Another piece of evidence is that harbour seal pups have calls that are not used after weaning. This would suggest that their purpose is to maintain contact with the mother (Sauvé et al 2015). But can mothers recognise the calls as their pups?

Firstly, can the mothers recognise the individual vocal stereotypy (ie: the unique sound of an individual)? Then, can she recognise the call that changes with age, and with the environment (eg: influence of wind and waves)? Sauvé et al (2015) set out to answer these questions by studying two harbour seal colonies on the St Lawrence River estuary, Canada.

Maternal attraction calls were recorded from seventy-seven temporarily captured pups in the 2013 breeding season for use in the playback experiment. This involved playing in the air and underwater simultaneously twenty-one females the calls of their own pup and a non-related pup (figure 4.5). The mother's response was scored by observers as the number of looks with the head out of water the mother made towards the loudspeaker playing the call, and the speed of approaching the loudspeaker. The mothers were significantly more responsive to the call of their own pup than an unrelated pup. This indicated that mothers could recognise their pup's call.

The "maternal protection level" was rated based on how close the mother remained to the pup in the water before the playback experiment. Highly protective mothers responded to both types of calls equally. Sauvé et al (2015) stated: "The absence of preferential response to calls of their own pup by highly protective females might be attributable to their hormonal status (lactogenic and sex steroid hormones...), bold personality and related strong motivation to reunite with their pup, which may incite them to pay less attention to vocalisation characteristics and to react strongly to any pup

¹⁵ Social recognition varies between gender, and within gender (appendix 4C).

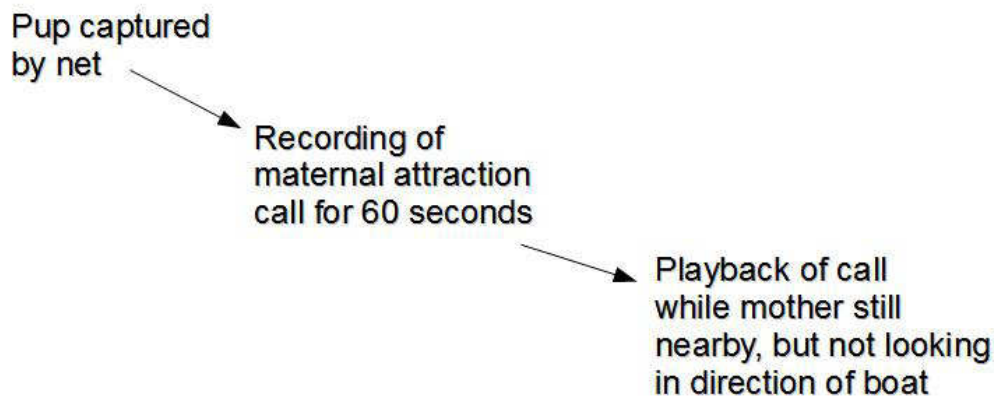


Figure 4.5 - Basic procedure of Sauv   et al (2015).

vocalisation heard when searching for their young" (p116). Such mothers have higher weaning success, but risk the cost of confusion (ie: caring for a non-related pup) (Sauv   et al 2015).

The difference in age between the call recording and playback had no effect on maternal response. This suggested that "females retain older versions of their offspring vocalisations despite modifications throughout rearing" (Sauv   et al 2015 p116).

The researchers also recorded the mother-pup reunion calls at the two seal colonies. The colonies varied in the amount of wind, which would affect the calls. Playback experiments were not performed, but it was speculated that the mothers could recognise the pup's call despite differences in weather conditions.

Species	Breeding colony density	Mother away foraging during lactation	Pup mobile during lactation	Vocal recognition
Northern elephant seal	High	No	No	Yes
Weddell seal	Medium	Yes	Yes	No
Hawaiian monk seal	Low	No	No	No
Harbour seals	Low	Yes	Yes	Yes

(Based on Sauv   et al 2015 table 4 p117)

Table 4.1 - Maternal vocal recognition in four phocid species and factors involved.

APPENDIX 4A - IMMUNE-CHALLENGED MALES

A male faces two challenges - a pathogen (immune challenge) and another male - when seeking a female. How does the former affect the latter?

Adamo et al (2015) used crickets (*Gryllus texensis*) to answer this question. Males have a stereotypical series of aggressive behaviours that increase in intensity during a fight, and so can be scored relatively easily for intensity, and who wins and loses.

The males, originally collected near Austin, Texas, were divided into three groups for the immune challenge variable - injection of heat-killed bacteria ¹⁶ (immune-challenged (IC) group), injection of placebo ¹⁷ (sham-injection group), or control group. Male fights were arranged between two individuals from the same group, or versus the control group, and in the presence of a female, a beetle ¹⁸, or unexposed.

IC crickets were significantly less likely to defeat controls 90 minutes after injection ¹⁹, but this was not the case five minutes or 24 hours after injection. Adamo et al (2015) felt that this was "suggesting a link between activation of the immune response and changes in aggressive behaviour".

However, IC crickets won more fights at ninety minutes post-injection when a female present. This showed that IC crickets were not too debilitated to win, rather it "supports the concept that males do not fight to the limit of their ability during every agonistic encounter, but make strategic allocations of effort" (Adamo et al 2015). This behaviour fits with the "terminal reproductive investment" strategy (Pölkki et al 2013) - ie: "forgoing the option of increased survival for increased reproductive possibilities" (Adamo et al 2015). This strategy only works if females do not avoid mating with IC males.

Adamo et al (2015) summed up: "Vigorous fighting leads to a decline in disease resistance in *Gryllus texensis*, suggesting that males cannot maximise defences against both competitors and pathogens simultaneously. Male crickets appear to trade off the ability to defeat pathogens for the ability to defeat competitors (ie: terminal reproductive investment), but only if an immediate reproductive payoff is possible (ie: in the presence of a female). However, when no immediate payoff is available, males reduce their aggressive motivation. In other words, defence against pathogens has priority

¹⁶ This was to induce "sickness behaviours" like illness-induced anorexia (Adamo et al 2015).

¹⁷ This was a control for the effect of the injection on behaviour.

¹⁸ To control for another presence's effect on the males.

¹⁹ Peak time for effect of injection on immune system.

when the reproductive payoff for fighting becomes less likely. Motivation is a key factor in determining the outcome of aggressive encounters in male crickets and appears to be the method by which male crickets mediate their trade-off between investment in pathogen defence and investment in reproduction" (p160).

APPENDIX 4B - HONEST SIGNALS

Intra-sexual competition (ie: competition between individuals of the same sex) is behind a lot of behaviour. Indirect signals, like body size, reduce the need for costly fights between rivals. Scent marking is an indirect signal, which can communicate the social status, reproductive status, and health of the depositor through aspects like mark density, refreshment rate, and distribution (Sharpe 2015).

Sharpe (2015) believed that how far off the ground the scent was deposited by mammals was also important. The height of the mark is an honest signal of size of the depositor in the case of leg-cocking urination (eg: grey wolves), for instance, or where anal-glands are rubbed against a surface (ie: height of mark reflects depositor's body height). However, "bluffing" does occur. For example, small mongooses use strategies to place their scent higher (eg: balancing on tip-toes or dangling down from above) (Sharpe 2015).

The dwarf mongoose (*Helogale parvula*) uses handstand-marking where the individual balances on their forepaws, and smears anogenital secretions as high as possible on a vertical object. Sharpe (2015) found that females paid more attention to higher markings in an experiment in Phuza Moya Private Game Reserve in north-east South Africa. She collected scent samples from different groups of animals, and then placed a composite scent at 10 cm and 16 cm above the ground. The average height for mongoose deposits is 14 cm above the ground. The time spent sniffing the deposit was the measure of interest. Ten males and ten females were tested with one week between conditions. Control scent using water was also placed at the same heights.

The male mongooses did not differ in their interest based on height (mean: 6.5 secs for high vs 5.3 for low scent), while female mongooses spent significantly longer sniffing the high scent (5.9 vs 2.4 secs for low scent).

APPENDIX 4C - SOCIAL RECOGNITION DIFFERENCES

Blocker and Ophir (2015) found that monogamous pair-bonded, but not single, prairie vole (*Microtus ochrogaster*) males could recognise non-mate females,

which suggested "a shift in cognitive behaviour after pair bond formation".

In their experiment, a social recognition test (habituation/dishabituation paradigm; Thor and Holloway 1981) was used with eleven pair-bonded and ten single males. The animals were individually presented with an unfamiliar female in an adjacent chamber to become familiar with. There was no contact, but auditory and olfactory information was available. This was done four times with the same female (habituation phase). Then the male was presented with a new unfamiliar female (dishabituation phase). The social recognition score was the difference in time in investigating the familiar and the unfamiliar female. The larger the score, the greater the degree of social recognition (ie: little time for familiar female and longer for unfamiliar).

Already pair-bonded males had significantly higher social recognition scores than the single (non-pair-bonded) males. Blocker and Ophir (2015) explained the findings thus: "...paired animals become more sensitive to sensory cues necessary to discriminate between unfamiliar females. Indeed, it is plausible that the overall experience of bonding (including increased behavioural interaction with a female, and any possible neurochemical changes resulting from the bonding experience that could alter perception, attention or other aspects of behaviour) could enhance the ability of paired males to distinguish between unfamiliar females" (p6).

The findings also fitted with an idea proposed by Zheng et al (2013): "...the hypothesis that establishing territories and tracking male conspecifics is particularly relevant for single males. They [Zheng et al] speculated that territorial behaviour appears to be important for single males in nature, and therefore tracking male identity would be necessary. On the other hand, since single males have not yet become attached to a female, tracking female identity should be relatively less important" (Blocker and Ophir 2015 p6).

REFERENCES

Adamo, S.A et al (2015) Effects of immune challenge on aggressive behaviour: How to fight two battles at once Animal Behaviour 105, 153-161

Blocker, T.D & Ophir, A.G (2015) Social recognition in paired, but not single, male prairie voles Animal Behaviour 108, 1-8

Bonato, M et al (2009a) Investment in eggs is influenced by male colouration in the ostrich, *Struthio camelus* Animal Behaviour 77, 1027-1032

Bonato, M et al (2009b) Male colouration reveals different components of immunocompetence in ostriches, *Struthio camelus* Animal Behaviour 77, 1033-1039

Gonzalez-Medina, E et al (2010) Parental and chick responses of laughing gulls (*Leucophaeus atricilla*) to increase of flight costs and brood

size Journal of Ornithology 151, 219-225

Gonzalez-Medina, E et al (2015) Regulation of breeding expenditure in the blue-footed booby, *Sula nebouxii*: An experimental approach Animal Behaviour 108, 9-16

Hamer, K.C et al (1998) Regulation of chick provisioning rate in Manx shearwaters: Experimental evidence and implications for nestling obesity Functional Ecology 12, 625-630

Kimwele, C.N & Graves, J.A (2003) A molecular genetic analysis of the communal nesting of the ostrich (*Struthio camelus*) Molecular Ecology 12, 229-236

Pölkki, M et al (2013) Dominance is not always an honest signal of male quality, but females may be able to detect the dishonesty Biology Letters 9, 20121002

Sauvé, C.C et al (2015) Mother-pup vocal recognition in harbour seals: Influence of maternal behaviour, pup voice and habitat sound properties Animal Behaviour 105, 109-120

Sharpe, L.L et al (2015) Handstand scent marking: Height matters to dwarf mongooses Animal Behaviour 105, 173-179

Thor, D.H & Holloway, W.R (1981) Persistence of social investigatory behaviour in the male rat: Evidence for long-term memory of initial copulatory experience Animal Learning and Behaviour 9, 561-565

Velando, A & Alfonso-Alvarez, C (2003) Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental effort in the blue-footed booby Journal of Animal Ecology 72, 846-856

Zheng, D-Z et al (2013) Social recognition is context dependent in single male prairie voles Animal Behaviour 86, 1085-1095

5. GROUPS

5.1. FISSION-FUSION GROUPS

Fission-fusion groups involve individuals or small sub-groups separating temporarily from the main group (to forage, for example), and later returning to it ²⁰. The membership of the sub-groups vary (Smith et al 2015).

One advantage of this behaviour is in reducing "consensus costs". When a whole group moves it requires agreement on the direction, timing, and destination ("consensus decision"; Conradt and Roper 2003), and potential conflicts may occur about these. Having a definite leader who make decisions (and imposes them) can help ²¹. On the other hand, fission-fusion groups allow individuals with different interests to go separate ways temporarily. However, there is the potential for conflict at the subsequent reunion (Smith et al 2015).

Smith et al (2015) explored reunion behaviour in observations of spotted hyenas (*Crocuta crocuta*) (figure 5.1) living in Masai Mara National Reserve (figure 5.2) in Kenya between 1996 and 2000. Individuals were identified by their unique spots, and social rank was scored based on outcome of dyadic agonistic interactions (conflict between two individuals - ie: who dominant and who submits). Observers, using vehicles, watched and followed the clan (main group), sub-groups and individuals from at least 200 metres away.



(Source: Mauro Mazzio)

Figure 5.1 - Spotted hyena in Masai Mara National Reserve.

²⁰ Goodall (1986) called them "parties" in reference to her observations of chimpanzees.

²¹ Flack et al (2006) found that the removal of high-ranking individuals who "police" the group reduced cohesion in pig-tailed macaques (*Macaca nemestrina*).



(Drawn with MapCreator 2.0)

Figure 5.2 - Location of Masai Mara National Reserve.

Focusing on reunions, the first social interaction of the arriving hyena(s) with a group member was categorised as "affiliative" (eg: greetings, sniffing, grooming), "aggressive" (eg: snap, bite, chase), "unsolicited appeasement" (eg: submissive posture, head bobbing), or "no obvious interaction". The five minutes before (baseline) and the five minutes after reunion were closely watched.

In total, there were over 4200 hours of observations, including around six thousand reunions (usually a returning single individual; 80% of cases). Affiliative interactions at reunion were most common (where an interaction was categorised), and the returning hyena(s) was more likely to be responsible for initiating them rather than receiving them (eg: 70% of greetings). Aggressive reunions were more common when food present.

Returning individuals who greeted others were nearly eight times less likely to fight than non-greeting returners. Smith et al (2015) summed up: "arriving hyenas whose first social interaction at reunions was a greeting were more protected from subsequent aggression during the post-fusion period than were arriving hyenas that failed to first greet those same conspecific at reunions on different occasions. Specifically, arriving hyenas received significantly less aggression during the post-fusion periods at sessions when they first

initiated a greeting with a newly joined group member than at sessions when their first social interaction did not involve a greeting" (p194).

In terms of the "consensus decision" about moving, the researchers found no evidence that "leaders" communicated or coerced others (ie: "passive leadership"). Because the "leaders" were usually high ranking females, Smith et al (2015) suggested: "Travelling hyenas likely rely upon localised rules, such as 'follow adult females that outrank me'. Thus, despite their apparent social complexity, hyena groups may in fact represent 'self-organised' fission-fusion systems (Camazine et al 2003). That is, hyena clans appear to lack any central authority imposing movement decisions. Instead, as in self-organised flocks of birds or crowds of humans..., coordinated movements appear to be based on localised decisions, which in turn produce complex fission-fusion dynamics" (p196) ²².

In terms of other species, most primates and ungulates are led by females and do not use coercion (eg: goat, giraffe), while males who herd female mates use coercion (eg: hamadryas baboon, musk ox) (Smith et al 2015).

Movement by an individual is an important part of consensus decisions, particularly in the case of predation risk. A sudden movement away from the group by an individual could indicate a predator (true positive), to which the whole group needs to react. This is seen in bird flocks and fish schools. But an individual may make a mistake (false alarm), which could transmit to the whole group (producing a false positive - run away when no predator). The consequence of ignoring a true positive, though, is obvious.

How does an individual in a group distinguish a true or false alarm? One possibility is a quorum threshold (Wolf et al 2013). For example, running away from a group is taken as a true alarm of predation by the whole group when a certain number of members of the group are showing this behaviour.

Clement et al (2015) found a quorum of about a quarter of group members was the minimum to cause the whole group to escape in an experimental game with students. A group of fifteen students stood in a line and looked at a slide showing 144 fish for two seconds. Within the school of fish was one odd one, either

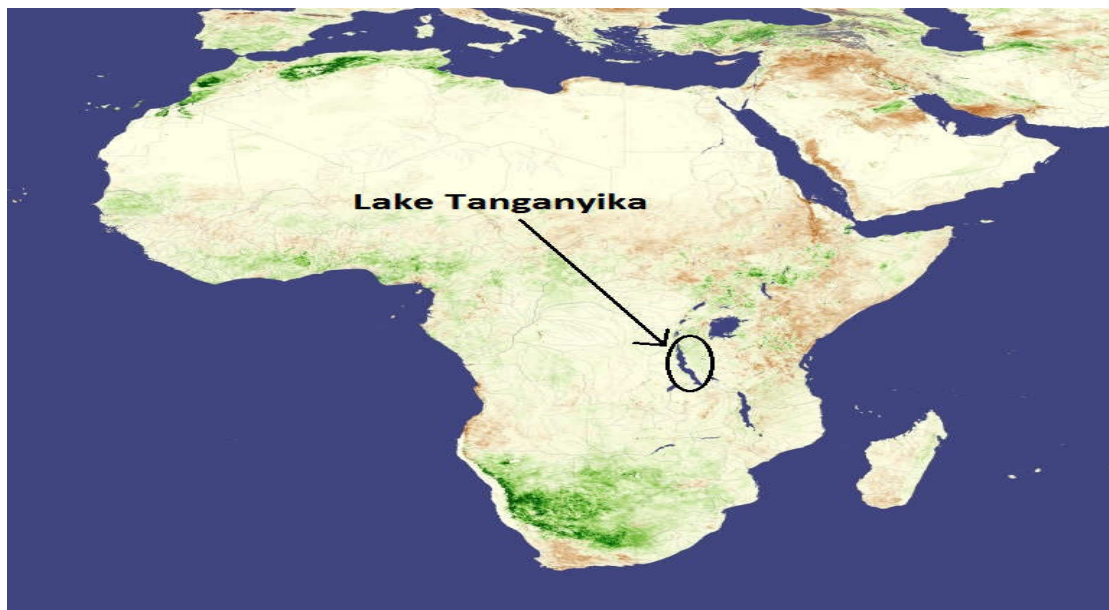
²² Large aggregations, like fish shoals, do not need a leader. They have "leadership by numbers" (Couzin et al 2005), where "only a few informed individuals are present and all group members adhere to a few simple rules of movement" (Ihl and Bowyer 2011 p819). Prins (1996) described "voting" by female African buffalo, who stood with their bodies positioned towards the preferred direction of travel during a group resting period.

designated as the predator or as harmless. Each student made the decision as to whether the odd fish was a predator by stepping forward or standing still if harmless.

5.2. SUBMISSIVE BEHAVIOUR

The use of submissive behaviour reduces costly conflict and is key to group stability. But this may not be so in larger social groups because "groups living in densely populated areas may have a greater ability to attract new members from neighbouring groups, which may decrease the importance of current members and consequently, decrease dominant tolerance of subordinate behaviour... Therefore, regardless of a subordinate's effort to moderate conflict, dominants may not reduce their policing or punishment of subordinates when there is a low cost to losing current subordinates" (Hellmann et al 2015 p56). On the other hand, subordinates may be less willing to be submissive if there are neighbouring groups available to join. The size of the group and the number of groups available to join are part of the "social landscape" (Hellmann et al 2015).

Hellmann et al (2015) showed the importance of this in their field experiment with co-operatively breeding cichlid fish (*Neolamprologus pulcher*) (appendix 5A) (found in Lake Tanganyika in East Africa) (figure 5.3). The experiment was performed in Kasakalawe Bay, Zambia (southern end of Lake Tanganyika) at a depth of 10-12 metres. The researchers used SCUBA.



(Source: NASA courtesy photo; in public domain)

Figure 5.3 - Location of Lake Tanganyika in Africa.

A high-ranking subordinate group member was removed temporarily for four hours from a group (or five minutes in the control condition), and then the aggression towards them was measured on return. Half of the removed fish were injected with the hormone isotocin (IT) which increases submissive behaviour (eg: tail quivers, submissive postures) (and the other half a saline solution as the control).

It was predicted that returning subordinates would receive more aggression in large than smaller groups and where there were more neighbouring groups. This was supported by the data.

It was also predicted that returning IT-injected fish would receive less aggression from dominant individuals than controls. The opposite was found. The IT group received over twice as much aggression as controls (eg: bite, ram). The researchers did not find, however, any less submissive behaviour by subordinates in the larger groups or where more groups were available.

Hellmann et al (2015) said: "We are uncertain why the IT-treated fish received more aggression from their focal group than the fish treated with saline in the removal treatment. It is possible that subordinates that received IT may have responded inappropriately to the social conflict induced by the removal. It is possible that individuals that received IT were inappropriately submissive upon return and therefore, were perceived to be of a lower status than they actually were" (p60).

5.3. SEX DIFFERENCES

In mammal species with sex-biased dispersal, it is usually the males who leave their natal habitat. Females benefit from kin support and "societies" often develop around females and their offspring. Females more than males form stronger and longer lasting social bonds (Foerster et al 2015).

Chimpanzees are different to this typical pattern with female-biased dispersal. However, this does not mean that female chimpanzees do not have strong non-kin social relationships. Foerster et al (2015) analysed the data collected from observations of chimpanzees at Gombe National Park in Tanzania for over thirty years. Data on associations between individuals were available for 1974 to 2011, and grooming behaviour for 1978 to 2011. Grooming (contact affiliation) was taken as a measure of a social relationship.

Female chimpanzees had distinguishable relationships with other females, usually kin. Non-kin mothers of

immature males associated together more than expected ²³, and mothers of immature females less than expected.

- Grevy's zebras (*Equus grevyi*) are more selective in their association choices and form stable cliques as well as homophily by females based on reproductive state. This is not so with the close related equid, onagers (or Indian wild ass) (*Equus hemionus khur*) (figure 5.4) who have more fluid associations. The difference may, in part, be due to the habitat of the two species - onagers live in open desert and Grevy's zebras in bushier areas. It is harder for the latter to find other individuals and groups to associate with. Also the predation risk is higher for the Grevy's zebra (which again would encourage staying in a stable group) (Sundaresan et al 2007).
- The researchers used on observations of 28 Grevy's zebras in Laikipia, Kenya, and twenty-nine onagers from the Little Rann of Kutch (desert) in Gujarat, India.

Table 5.1 - Details of Sundaresan et al (2007).



(Source: Asim Patel)

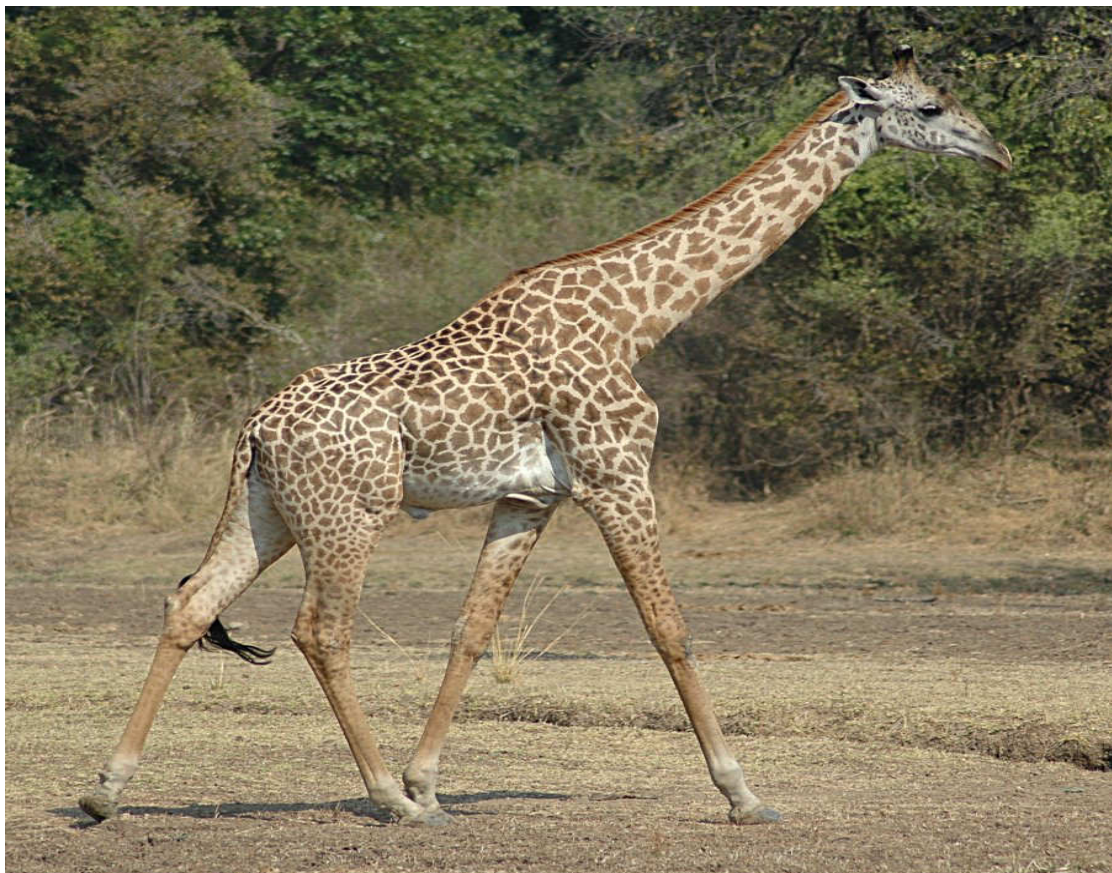
Figure 5.4 - Onagers in Little Rann of Kutch.

²³ This is homophily - "the tendency to bond with similar others" (Foerster et al 2015) - and it has been reported in other species like Grevy's zebra (Sundaresan et al 2007) (table 5.1).

5.4. LEADERS

"Leader" usually refers to the individual at the front of a group travelling in one direction (Berry and Bercovitch 2015). They may pay a cost, for example, in increased exposure to predators (Ihl and Bowyer 2011) ²⁴.

Berry and Bercovitch (2015) analysed forty-one years of data (1971-2012) on Thornicroft's giraffes (*Giraffa camelopardalis thornicrofti* ²⁵) (figure 5.5) in South Luangwa National Park, Zambia. There were sixteen females and thirty-six males. Individual animals were identified by unique blotch patterns.



(Source: Jpatokal)

Figure 5.5 - Thornicroft's giraffe in Zambia.

²⁴ During the V-shaped or echelon formation of birds flying, the leader uses more energy while the followers can achieve energy saving by the aerodynamic up-wash produced from the bird in front. Voelkl et al (2015) found that a flock of fourteen Northern bald ibis (*Geronticus eremita*) showed co-operation in turn-taking in being the lead bird. The hand-reared birds were observed and their flight logged via GPS across Austria. Pairs of birds matched the time they spent in the wake of others by frequent switches of leader. This is evidence of reciprocal altruism between unrelated individuals (In Brief 2015).

²⁵ A distinct sub-species of giraffe in this area of Africa (Berry and Bercovitch 2015).

The leader was the individual in the front position of a single file (linear) progression of a group of four or more animals ²⁶. Twenty-three instances of such movement were recorded (table 5.2), and in only two of them was the leader male. Of the twenty-one cases of female leader, the age was known in nineteen, and most often (17 cases) it was the oldest female (matriarch). The average size of the moving group was five, and randomly the oldest female would be the leader in 20% of cases. Thus, there was a significant difference between the number of times the oldest females were observed as leaders and chance.

- On June 30, 1993, at 1940 h, we recorded five giraffe in open woodland near Mfuwe Lagoon, with four of them lying on the ground. An 18.8-year old female was standing next to them. She was the oldest female in the herd and as she moved away, the others stood up and followed. In this case, the progression order was recorded and the leader was followed by two sisters, one aged 10 and the other aged 3, an unrelated male, and the 13-month-old son of the leader female. They moved in a single file for 5 min, at which time the observations terminated.

(Source: Berry and Bercovitch 2015 pp177-178)

Table 5.2 - Example of observation of Thornicroft's giraffes.

Four hypotheses for this behaviour were tested with the data:

i) Random - The herd members were not following a leader, but moving randomly in the same direction. Linear progressions are uncommon, so this hypothesis is unlikely to be correct.

ii) Bonds - It was dependent offspring following their mother. Again this was unlikely because adult daughters were followers. Berry and Bercovitch (2015) stated: "We conclude that mother/offspring bonds contributed to the finding that matriarchs are often leading herd progressions, but such bonds cannot account for the ubiquity of the pattern, given that progressions contained non-kin, as well as genetic relatives other than mothers and offspring" (p180).

²⁶ Concentrating on groups of at least four individuals with at least two adults, Berry and Bercovitch (2015) defended their decision: "Although we may have underestimated the actual number of herd progressions by omitting any questionable observations, deleting progressions involving males following oestrous females, and restricting analysis to cases that excluded only a cow and her immature calves, we have strengthened the approach by adopting a conservative perspective providing insights into giraffe herd movements, given their flexible social system" (p177).

iii) Predator protection - A study by Bashaw (2003 quoted in Berry and Bercovitch 2015), where the sound and smell of lions was manipulated, found that the oldest females were most often the leaders. For their data, Berry and Bercovitch (2015) admitted that "predator risk probably influences joining a progression of giraffe, but cannot account for the ubiquity of matriarchal leadership in such progressions" (p180).

iv) Resource learning - Berry and Bercovitch (2015) felt that the knowledge of the matriarch about resources (including water, food, and predator "hotspots") was the main reason for being followed.

Among African elephants, for example, the oldest females lead the families to distant water sources during a drought (Foley et al 2008).

While post-menopausal killer whales (*Orcinus orca*) (figure 5.6) were more likely to lead the group than other adults females and males, especially when food (Chinook salmon) was in short supply (Brent et al 2015)²⁷. This supports the explanation for the evolution of the menopause that older females have important knowledge for the group (Diamond 2001) (ie: "post-reproductive females may boost the fitness of kin through the transfer of ecological knowledge"; Brent et al 2015)²⁸.



(Source: Leigh Calvez; <http://www.insidebainbridge.com/2011/08/21/lessons-from-the-shore-going-with-the-orca-flow/>)

Figure 5.6 - Older female orca called "granny" off Washington State, USA.

²⁷ This was based on more than 750 hours of video footage of killer whales in coastal waters off British Columbia and Washington State (since 1976), which produced observations of 102 individuals (identified by fin shapes, saddle patches, and nicks/scratches).

²⁸ Females breed between 12-40 years old, but can live into their 90s, while males rarely survive beyond fifty years old (Brent et al 2015).

Another theoretical prediction was supported that mothers will invest more in sons than daughters because the former have higher reproductive potential (Johnstone and Cant 2010). Adult males were observed by Brent et al (2015) to be more likely to follow their mothers than adult females. Further support for this difference was reported by Foster et al (2012), who recorded a nine-fold increase in mortality risk for adult sons after the death of their mothers as compared to three-fold for adult daughters.

Ihl and Bowyer (2011) reported observations of twenty-four mixed-sex groups of musk oxen (*Ovibos moschatus*) (figure 5.7) in Cape Krusenstern National Monument, Alaska in 2002 via a small aeroplane and on foot. Adult females were more likely to be "initiators of group activity" (ie: first to rise after a resting bout and begin in new activity), and did so significantly more often than chance, while males succeeded in initiating activity by being aggressive towards females.

The same was true for "foraging-bout movements" (defined as "when >80% of the herd was moving slowly in the same direction while foraging") (Ihl and Bowyer 2011).



(Source: Martin Bayer)

Figure 5.7 - Musk ox.

5.5. SOCIAL RELATIONSHIPS

Social relationships between individual animals vary in content (eg: affiliation or conflict), quality (eg: intensity of aggression), and patterning (eg: frequency of interactions)²⁹. These differences are influenced by non-dispositional factors like age, sex, kinship, and position in social hierarchy (rank). So, for example, females prefer high-quality relationships (ie: more affiliative than agonistic) with alpha group members because of the better protection and access to food that accompanies it (Morton et al 2015).

But non-dispositional factors cannot explain all social relationships (ie: predict partner choice). Individual differences or "personality" (consistent behaviour, affect and cognition across time and contexts) may be important. Similar personalities (however that is measured) have been shown to predict affiliative social relationships more than different personalities in a number of species (Morton et al 2015). For example, pair bonding in eastern bluebirds (*Sialia sialis*) between individuals similar in aggression (Harris and Siefferman 2014; appendix 5B)³⁰, or group member affiliation of individuals with similar in the trait of Adaptability (eg: flexibility) in rhesus monkeys (*Macaca mulatta*) (Weinstein and Capitanio 2008).

There is an evolutionary basis to similarity. For example, similarity of mates in aggression produces better quality offspring in great tits (*Parus major*) (Both et al 2005), while guppy (*Poecilia reticulata*) mates similar in boldness have greater reproductive success than dis-similar mates (Ariyomo and Watt 2013).

The problem with many studies is controlling for non-dispositional factors when looking for similarities in personality. Morton et al (2015) pointed out: "Controlling for non-dispositional factors is critical for several reasons. For instance, partner similarities in bold or aggressive personality traits may reflect attraction towards individuals that are similar in rank... Additionally, as these (and other) personality traits are heritable,... partner similarities in personality may be proxies for the degree of relatedness between pair members" (p164).

²⁹ Positive social relationships are important even among apparent competitors (Dugatkin and Hasenjager 2015). For example, male long-tailed mankin (*Chiroxiphia linearis*) compete in song and dance for females at lek. But only highest-ranking males get this opportunity, and the individuals who become highest-ranking are well connected in terms of social network (Edelman and McDonald 2014).

³⁰ Assortative mating is choice of partner based on similarity, while disassortative mating is "a sort of division-of-labour" (Harris and Siefferman 2014).

Morton et al (2015) took this into account in their study of brown capuchin monkeys (*Sapajus* sp), where fifty-four hours of observation were made of eighteen individuals at the Edinburgh zoo in Scotland in 2011 (table 5.3). Relationship quality was calculated for pairs of individuals interacting (dyads) by subtracting negative aspects (eg: aggression) from positive aspects (eg: food sharing). High-quality relationships had more positive than negative aspects, and low-quality relationships the opposite.

- Focal sampling - watching each individual for ten minutes and scoring seven behaviours (eg: solitary, grooming).
- Continuous behaviour sampling - all incidences of aggression, coalitions, scrounging, and food sharing recorded.
- Intermittent behaviour sampling - at one-minute intervals, all other behaviours recorded (instantaneous sampling).

Table 5.3 - Observation sampling used by Morton et al (2015).

Each individual was rated on the Hominoid Personality Questionnaire (Weiss et al 2009), which covers fifty-four traits under five personality dimensions: Assertiveness (eg: aggressive vs submissive), Openness (eg: inventive), Neuroticism (eg: excitable vs cool), Sociability (eg: sociability vs solitary), and Attentiveness (eg: thoughtless). The rating was done by different observers at different times to give reliability.

Dyads with similar scores on the Sociability dimension had significantly better quality relationships as did pairs similar in Openness, while the other three dimensions were not significant. After controlling for age, sex, kinship, and rank, only Sociability was significant, while similarity in Neuroticism was associated with more affiliative relationships scores. The findings confirmed the importance of similarity for these dimensions (whether the pair were "high, low or somewhere in between on these traits") (Morton et al 2015).

5.6. SOCIAL SPIDERS

Spiders are usually assumed to be solitary, but there are social spiders that live in colonies, like the African desert social spider (*Stegodyphus dumicola*). They live in multi-female societies that can include several hundred spiders, and co-operate in web maintenance, prey capture, and care for offspring (showing task

specialisation ³¹) (Wright et al 2015).

Personality-based task differentiation (PBTD) is where the task specialisation is based on the individual differences ("personality") of the group members. For example, bolder social spiders (*Stegodyphus sarasinorum*) specialise in prey attack (Grinsted et al 2013), while less aggressive members of another species (*Anelosimus studiosus*) specialise in brood care (Wright et al 2014).

Wright et al (2015) studied colonies of *Stegodyphus dumicola* in the laboratory and in the field in South Africa. Initially, in the laboratory, the boldness of each spider was measured by their speed to resume movement after two rapid puffs of air to mimic a flying predator. The spiders responded by becoming static, and bolder individuals started to move again after a short time. Spiders were put in groups of ten or thirty based on four types - all bold, all shy, half and half, or all "median" boldness.

Each colony was tested by stimulating the web as if prey captured. The most individuals attacked from the all-bold colonies, but there was no difference in speed of response between the colonies. Larger individuals were more likely to be involved as were those in smaller colonies. The collective foraging behaviour was due to a combination of group size, body size of members, and individual boldness.

Then the colonies were moved outside the laboratory, and the researchers simulated an attack to produce escape behaviour. There was no difference in this behaviour between the colonies based on size of colony or individual members.

Settepani et al (2015) did not find PBTD in a sub-social spider species (*Stegodyphus tentoriicola*). Sub-social species live together until adulthood, when they become solitary. The young stay with the mother after hatching and then consume her (matrphagy).

The researchers studied juvenile spiders collected near Kimberley, South Africa, in 2013. After testing each spider for boldness with the puff of air test, they were placed in colonies of twenty individuals. An individual's participation in a simulated prey capture was measured (ie: First to Attack, and React at Time of Attack). Individual boldness, which did not show reliability in measurement over seven days, was not related to participation in prey capture. Only "sitting close to stimulus" significantly predicted First to Attack and React at Time of Attack.

³¹ Task specialisation can emerge in a group. For example, halictine bees, who are usually solitary, show task specialisation (eg: excavation or nest guarding) when experimentally forced into a social group (Jeanson et al 2008).

APPENDIX 5A - CICHLID FISH

Cichlids (figure 5.8), with over 2500 species, are mostly found in Lakes Victoria, Malawi, and Tanganyika in East Africa, but also in South Asia and the Americas (Meyer 2015).



(Source: User:Pburka; in public domain)

Figure 5.8 - Cichlids of Lake Malawi.

Cichlids in Lake Victoria are a "textbook example" of "adaptive radiation" - where "one lineage spawns numerous species that evolve specialisations to an array of evolutionary roles" (Meyer 2015).

Examples of specialisations include the evolution of asymmetrical jaws (ie: opening to left or right) for those fish that feed on the scales of other fish, or enlarged lips for fish that find prey in rock crevices (Meyer 2015).

But such ultra-specialised adaptation can be risky if the particular food source is lost. Cichlids overcome this problem by having two sets of jaws (one in the mouth and one in the throat). The mouth jaws can become specialised while the throat jaws can deal with any food type. "In other words, they can evolve a specialisation but remain generalists at the same time in case their preferred food runs out or a better option becomes available" (Meyer 2015 p59).

Meyer (2015) outlined a number of genetic mechanisms that have aided the evolutionary diversity:

- i) Abundant genetic mutations.
- ii) High rate of gene duplication and thus errors in DNA replication quickly spread.
- iii) "Jumping genes" (transposable elements) - sequences of DNA that jump to a new position in the genome during replication.
- iv) Mutations in the DNA in part of the genome that tends to not mutate.
- v) More new micro-RNAs, which inhibit genes, than other fish.

APPENDIX 5B - HARRIS AND SIEFFERMAN (2014)

Eastern bluebirds (figure 5.9) are obligate secondary cavity-nesting birds, which means that they nest in cavities in rocks excavated by other birds. Such cavities are in short supply and territorial defence against other bluebirds and tree swallows is important. However, there is variation in this behaviour between individual birds.



(Source: Lee R DeHaan)

Figure 5.9 - Male eastern bluebird.

Harris and Siefferman (2014) studied bluebirds in sixty-three nest boxes in Watauga County, North Carolina, USA in the 2012 breeding season. Reproductive success was measured by weight of nestling at thirteen days after hatching, and number of fledglings (ie: young that survived to leave the nest at between 15 and 21 days). Territorial aggression was scored as the time taken to respond to another bird placed in their territory by the researchers. This is known as a simulated territorial intrusion.

Breeding pairs that were similar in aggression produced the heaviest nestlings, especially in areas of high competition for nests, but the total number of offspring fledged was not significantly related to similarity. The most successful parents were both high or both low in aggression (table 5.4).

MALE	MORE AGGRESSIVE FEMALE	LESS AGGRESSIVE FEMALE	SIGNIFICANT
Most aggressive one-third	28	24	yes
Middle one-third	26	26	no
Least aggressive one-third	20	27	yes

Table 5.4 - Pattern of similarity between mates on aggression and approximate nestling mass at fourteen days (g).

Harris and Siefferman (2014) explained the findings, thus. Two highly aggressive birds can defend better quality territory (ie: more food available; less risk of nest predators), while two non-aggressive individuals may be able to forage more efficiently (even in low-quality areas). Alternatively, two similar "personalities" may be better at co-ordinating parental care (one parent forages while the other stays at nest).

Harris and Siefferman (2014), however, were cautious: "it is difficult to know if the behaviour of the individual changes after mating or if behaviour is consistent and personality is an important criteria for mate choice. In this study, we measured territorial aggression, which may be a component of personality, but individuals in a pair that behave similarly may be simply responding to one another".

The researchers also accepted two other limitations to their work - (i) study based on nest boxes rather than natural nesting cavities (where competition is even more intense), and (ii) no details of survival of offspring

after fledging.

REFERENCES

- Ariyomo, T.O & Watt, P.J (2013) Disassortative mating for boldness decreases reproductive success in the guppy Behavioral Ecology 24, 1320-1326
- Berry, P.S.M & Bercovitch, F.B (2015) Leadership of herd progressions in the Thornicroft's giraffe of Zambia African Journal of Ecology 53, 2, 175-182
- Both, C et al (2005) Pairs of extreme avian personalities have highest reproductive success Journal of Animal Ecology 74, 667-674
- Brent, L.J et al (2015) Ecological knowledge, leadership, and the evolution of menopause in killer whales Current Biology 25, 6, 746-750
- Camazine, S et al (2003) Self-Organisation in Biological Systems Princeton, NJ: Princeton University Press
- Clement, R.J.G et al (2015) Information transmission via movement behaviour improves accuracy in human groups Animal Behaviour 105, 85-93
- Conradt, L & Roper, T.J (2003) Group decision-making in animals Nature 421, 155-158
- Couzin, I.D et al (2005) Effective leadership and decision-making in animal groups on the move Nature 433, 513-516
- Diamond, J (2001) Unwritten knowledge Nature 410, p521
- Dugatkin, L.A & Hasenjager, M (2015) The networked animal Scientific American June, 39-43
- Edelman, A.J & McDonald, D.B (2014) Structure of male co-operation networks at long-tailed manakin leks Animal Behaviour 97, 125-133
- Flack, J.C et al (2006) Policing stabilises construction of social niches in primates Nature 439, 426-429
- Foerster, S et al (2015) Social bonds in the dispersing sex: Partner preferences among adult female chimpanzees Animal Behaviour 105, 139-152
- Foley, C et al (2008) Severe drought and calf survival in elephants Biology Letters 4, 541-544
- Foster, E.A et al (2012) Adaptive prolonged post-reproductive life span in killer whales Science 337, p1313
- Goodall, J (1986) The Chimpanzees of Gombe: Patterns of Behaviour Cambridge, MA: Belknap Press
- Grinsted, L et al (2013) Individual personalities shape task differentiation in a social spider Proceedings of the Royal Society B: Biological Sciences 280, 20131407
- Harris, M.R & Siefferman, I (2014) Interspecific competition influences fitness benefits of assortative mating for territorial aggression in eastern bluebirds (*Sialia sialis*) PLoS ONE 9, 2, e88668 (Freely available at <http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0088668>)
- Hellmann, J.K et al (2015) Group response to social perturbation: Impacts of isotocin and the social landscape Animal Behaviour 105, 55-62
- Ihl, C & Bowyer, R.T (2011) Leadership in mixed-sex groups of musk oxen during the snow-free season Journal of Mammalogy 92, 4, 819-827

In Brief (2015) The mystery of the bird flying out front New Scientist 7/2, p16

Jeanson, R et al (2008) Division of labour and socially induced changes in response thresholds in associations of solitary halictine bees Animal Behaviour 76, 593-602

Johnstone, R.A & Cant, M.A (2010) The evolution of menopause in cetaceans and humans: The role of demography Proceedings of the Royal Society B: Biological Sciences 277, 3765-3771

Meyer, A (2015) Extreme evolution Scientific American April, 56-61

Morton, F.B et al (2015) Capuchin monkeys with similar personalities have higher-quality relationships independent of age, sex, kinship and rank Animal Behaviour 105, 163-171

Prins, H.H.T (1996) Ecology and Behaviour of the African Buffalo London: Chapman & Hall

Settepani, V et al (2015) Temporarily social spiders do not show personality-based task differentiation Animal Behaviour 105, 95-102

Smith, J.E et al (2015) Collective movements, leadership and consensus costs at reunions in spotted hyenas Animal Behaviour 105, 187-200

Sundaresan, S.R et al (2007) Network metrics reveal differences in social organisation between two fission-fusion species, Grevy's zebra and onager Oecologia 151, 140-149

Voelkl, B et al (2015) Matching times of leading and following suggest co-operation through direct reciprocity during V-formation flight in ibis Proceedings of the National Academy of Sciences, USA 112, 2, 2115-2120

Weinstein, T & Capitanio, J (2008) Individual differences in infant temperament predict social relationships of yearling rhesus monkeys, *Macaca mulatta* Animal Behaviour 76, 455-465

Weiss, A et al (2009) Assessing chimpanzee personality and subjective well-being in Japan American Journal of Primatology 71, 283-292

Wolf, M et al (2013) Accurate decisions in an uncertain world: Collective cognition increases true positives while decreasing false positives Proceedings of the Royal Society B: Biological Sciences 280, 20122777

Wright, C.M et al (2014) Animal personality aligns task specialisation and task proficiency in a spider society Proceedings of the National Academy of Sciences, USA 111, 26, 9533-9537

Wright, C.M et al (2015) Personality and morphology shape task participation, collective foraging and escape behaviour in the social spider, *Stegodyphus dumicola* Animal Behaviour 105, 47-54