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Breeding Aggregations and Other Groups

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A complete listing of his writings at <http://psychologywritings.synthasite.com/>. See also material at <https://archive.org/details/orsett-psych>.

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## 1. INTRODUCTION

Earley and Dugartkin (2010) defined a social group as "a collection of individuals that actively cluster together, exist in close proximity in both space and time, and engage in behavioural interaction; a social group also is a discrete unit that is distinct from other such groups" (quoted in Macedo and DuVal 2018). One form of social group is "breeding aggregations", where individuals come together for a specific purpose.

But such sociality has both costs and benefits. It is assumed that the latter outweighs the former.

## 2. BIRDS AND THE HIDDEN LEK HYPOTHESIS

"Clustered breeding distributions" can be seen to "reflect spatially uneven resource distributions, as many individuals in a population choose the same high-quality sites" (Macedo et al 2018 p145). Grouping around concentrated patches of resources is an obvious advantage. But there are non-resource-based breeding clusters, which Macedo et al (2018) described as "the non-random distribution of individuals across the landscape, such that they are close together in a pattern that does not necessarily reflect resource distribution" (p145).

Macedo et al (2018) explored this in relation to birds in three contexts:

i) Coloniality - This is where individual territories are small and tightly packed with limited resources. It is suggested that coloniality evolved independently at least twenty times in birds, thus it must be advantageous (Macedo et al 2018). The key costs are increased competition for resources, risk of cannibalism and infanticide, and elevated transmission of pathogens and parasites. "Safety in numbers" needs to trump these costs (eg: protection from predators due to the dilution effect; increased opportunities for vigilance and alarm calls; inaccessible location for predators; mobbing of threats) (Macedo et al 2018).

Copulations with multiple partners is more frequent, for example, in colonial birds than solitary species. Though this is a cost to the cuckolded individual, and a benefit for the individual achieving extra-pair fertilisation (EPF). If enough individuals benefit, then

colony formation is favoured. However, Macedo et al (2018) argued that "in general, EPFs are not likely to be an important driver of coloniality, but rather a consequence of the high-density nesting situation" (p147).

ii) Lekking - Males usually cluster in small areas (called "arenas") to display to the visiting females. The aggregation is by males only for fertilisation, and females are entirely responsible for post-fertilisation elsewhere. "Classic" leks (ie: many males in small area with no defended resources) include in the Ugandan kob, and the greater sage grouse (DuVal et al 2018) (appendix A).

"Aggregations on landmarks" occur where there are limited suitable display areas (eg: forest clearings; hilltops), "exploded leks" are more dispersed, and "resource-based leks" "occur when males aggregate near resources that are critical for females" (Macedo et al 2018 p147).

"Leks are typically characterised by extravagant male displays, and by extreme sexual selection as mating success among displaying males is highly skewed" (DuVal et al 2018 p216).

Leks can be advantageous to the "best" males that attract the most matings, but producing a reproductive skew (eg: one male wire-tailed manakin was found to have sired 22 of 24 genotyped offspring; Ryder et al 2009). However, females may not all agree on the best males and/or mate with multiple males. This is "a safety measure against male infertility" (Macedo et al 2018 p148).

iii) Clustered territoriality in socially monogamous species - These have been called "neighbourhoods" or "loose" colonies, and involve larger resource-based territories that back onto each other (Macedo et al 2018). EPF is proposed as an advantage for females here, leading to greater offspring variety, but also potential mate replacements.

Wagner (1993) explained this context with the "hidden lek hypothesis" - ie: "a hidden lek is a cluster of territorial, socially monogamous pairs that aggregate primarily due to the fitness advantages females gain through EPC [extra-pair copulation]" (Macedo et al 2018 p149). Macedo et al (2018) felt that this model had not been fully assessed with a single species., though these researchers were collecting data on the blue-black grassquit (*Volatinia jacarina*). Note that in "classical

lekking", males provide no parental care, whereas they do according to this theory.

Macedo et al (2018) ended: "Mating systems have traditionally been classified into discrete categories, with socially monogamous and lekking mating systems regarded as resulting from very different sets of selective pressures. The hidden lek hypothesis adds a layer of complexity to the story, by illustrating that the dividing lines between different mating systems can be blurry" (p151).

### **3. IRRATIONAL MALE CRABS**

Brockmann et al (2018) made the comment that "on the surface, some mating decisions within breeding aggregations have no clear adaptive value and some appear maladaptive" (p178). For example, males choosing to join larger groups with many males competing for a female when there are smaller groups available. "When these opportunities are in close spatial proximity, it is even more difficult to explain" (Brockmann et al 2018 p178). These researchers suggested that it is our failure to understand when it is happening in breeding aggregations. They concentrated on the American horseshoe crab (*Limulus polyphemus*) and high tide spawning aggregations.

During new and full moon high tides in the spring in the eastern USA, a male and a female pair (which has formed in the sea) crawl onto the beach (in vast numbers). There are "large numbers of unpaired males that gather around spawning pairs to form mating groups... Satellite and paired males compete within the mating group to fertilise the eggs that the female is laying... The number of satellites around a pair (ie: satellite group size) varies widely; it is not uncommon at peak spawning to see four or more satellite males around a pair while at the same time other pairs are spawning nearby without satellites" (Brockmann et al 2018 p178) (figure 1).

Only two satellites within a large group have been found to achieve fertilisation success. Any more males have fertilisation success around 10% (Brockmann et al 2018). "One would expect mating groups to form according to an ideal free distribution... If males are free to move, then they should distribute themselves among mating groups so as to maximise their expectation of reproductive success. In general, this would predict that mating groups should be roughly equal in size,



(Source: Pos Robert, US Fish and Wildlife Service; public domain)

Figure 1 - Breeding pair and satellite male.

although individual differences among females may translate into variation in mating group sizes. For example, if some females are more fecund than others, then group sizes are predicted to be larger around the more productive females" (Brockmann et al 2018 p178).

Brockmann et al (2018) statistically modelled the ideal behaviour of males using observed data from Seahorse Key, Florida between 1993 and 2014. The number of pairs, unpaired males, unpaired females, mating groups, and satellites per group were counted. In total, there were 339 survey days.

Overall, the simulations could not provide rules that the males followed that made evolutionary sense. It seems that males are not choosy about which groups they join. The modelling produced many hypotheses to test with observations.

## 4. PRAIRIE VOLES

Theories about reproductive success assume an optimal size for a group depending on the type of social unit. For example, a female with a socially monogamous partner has greater reproductive success (eg: raise young to maturity) than a solitary female, while a female living with more than two adults gain even more benefits. On the other hand, there are species where female reproductive success declines as the group size increases, and single females have best success (Solomon and Keane 2018). How to make sense of such contradictions?

One answer may be to focus on individual species rather than seeking general rules. Solomon and Keane (2018) reported on the prairie vole (*Microtus ochrogaster*), where adult females breed in three different types of social unit - socially monogamous male-female pair, female without other adults, or "communal group" (males and females).

Female reproductive success (defined as, for example, offspring surviving to twelve or thirty days old) has been studied extensively in this species. For example, McGuire et al (2002) found, based on seven years of data, that females living in groups with three adults were more successful than females in groups with less or more than three adults. While Solomon and Crist (2008) estimated that lifetime reproductive success was much higher for females in male-female pairs than in groups with only one breeding pair (Solomon and Keane 2018).

Solomon and Keane (2018) analysed data on two natural populations of prairie voles in the USA collected between 2005 and 2010. Parentage of juveniles was assessed by genotyping from tissue samples of trapped individuals. There was no significant relationship between the three types of social units and female reproductive success (ie: number of offspring produced), although there was a non-statistically significant negative relationship between social unit size and reproductive success. This suggested, Solomon and Keane (2018) explained, that "female reproductive success decreases to some extent when social units become larger, although in our study, social unit size was not as important a factor in explaining female reproductive success as the persistence and residency status of females on the study site" (p200).

One methodological issue with studies is how reproductive success is measured - for example, number of



offspring produced, offspring survival for certain period or to breed themselves, or offspring quality (eg: body mass). Another issue is the sampling process (ie: the number of nests, and length of study) (Solomon and Keane 2018).

## 5. SOCIAL SPIDERS

Social spiders are an interesting group to study as it includes fewer than thirty out of nearly 47 000 described species of spider (Pruitt and Aviles 2018). Social spiders show co-operation and no aggression towards siblings. They differ from colonial spiders and sub-social species. "Colonial spiders aggregate together in conglomerate webs but maintain individual sub-territories within these aggregations; thus, individuals within these aggregations generally do not co-operate directly. Sub-social spiders live in co-operative family groups composed of a single mother and her offspring, but those offspring develop aggressiveness towards their siblings sometime in their development, and will disperse prior to their penultimate moult" (Pruitt and Aviles 2018 p155).

Social spiders co-operate in prey capture, group web construction, defence, and alloparenting. But why has this behaviour evolved, or, as Pruitt and Aviles (2018) asked it, "why are social spiders social?" (p156).

One answer is related to the environment where social spiders live in the main - neotropical rainforests. "These habitats are characterised by intense rain that damages spiders' webs..., frequent attacks by predatory ants... and the presence of large insect prey... In such environments group-living spiders enjoy the benefits of reduced per capita energy investment in web repair following rain... Colonies are also more likely to survive sieges by ants than individual spiders in a solitary web" (Pruitt and Aviles 2018 p156). Other social spiders are found in savannah habitats in southern Africa, Madagascar and India, and they face harsh conditions and some common problems with rainforests dwellers (eg: ant attacks) (Pruitt and Aviles 2018).

But there is a cost to the evolution of sociality, which may explain why so few species have evolved it, namely a decrease in aggression (ie: "social spiders (per capita) become less aggressive towards conspecifics, prey, parasites, predators, mates and so on"; Pruitt and Aviles 2018 p157).

High relatedness of colony members is another cost

(ie: low genetic diversity). Pruitt and Aviles (2018) described social spiders as "evolutionary and ecological losers... [They] are unsuccessful in terms of speciation..., geographical distribution..., and persistence at ecological or evolutionary timescales" (p158). Colonies can experience "boom-and-burst cycles of destruction and recolonisation... the result is that social spider colonies emerge at sites quickly and wink out at alarming rates, without apparent stability" (Pruitt and Aviles 2018 p158).

## **6. HONEST SIGNALLING**

Courtship, aggression and co-operation signals "appear to be generally honest, at least on average", noted Webster et al (2018; p168). But how to ensure, in evolutionary terms, that signals are honest?

In a lekking situation, for example, where males all show off their quality in a display, a low-quality individual who can "pretend" to be high-quality will gain breeding benefits. This would be dishonest signalling, and the "honest males" lose out, and so do females. There must be a reliable way for females to assess quality of males.

One possibility is that honest signalling evolved with a cost for the signaller that is too high for low-quality individuals. Zahavi (1975) described this idea in terms "handicap" (appendix B). For example, ornamental signals, like the male peacock's tail, make the owner more conspicuous to predators, less able mobile to escape, and/or less able to forage. So, the honest of the signal is maintained because of the high cost of such ornaments.

There are physiological and social costs. An example of a physiological cost is high testosterone. High testosterone is the basis of successful sexual signals, but requires high energy to maintain it or reduces the effectiveness of the immune system. A social cost is the response to the signal of conspecifics. A male signalling dominance may receive many challenges from other males, for instance.

Webster et al (2018) noted that "very few studies have tested the key prediction that physiological production costs differentially affect low-quality individuals over high-quality individuals" (p167). These researchers favoured social costs as driving honest signalling. For example, among red-backed fairy-wrens (*Malurus melanocephalus*), males with bright plumage (red-

black), a honest signal of quality as such males sire more offspring, receive more aggression (eg: territorial intrusion) from other males with red-black plumage than do non-conspicuous males (juveniles with brown plumage) or females (Webster et al 2018).

The evolution of honest signalling is possibly a combination of different costs (eg: Tibbetts 2014).

## **7. INTER-GROUP CONFLICT**

When social groups of animals compete, larger groups "frequently win... This correlation between competitive ability and group size is thought to be an important selective pressure favouring the evolution of sociality" (Strong et al 2018 p205). But what about the times that larger groups do not win? Factors like group stability, the age and experience of the members, and perceived value of the resource competed over have all been found to be important (Strong et al 2018).

An interesting variation is location of the conflict. In a study of white-faced capuchins, for instance, Crofoot et al (2008) found that "group size did confer a competitive advantage, but that this advantage was far more important at the periphery of a group's territory (where the costs of losing were relatively small) than near the centre (where the costs of losing were presumably larger)" (Strong et al 2018 p205).

Most studies of inter-group competition and conflict have involved social mammals, and there are few on social birds. For example, Seddon and Tobias (2003) found that group size was important in a playback experiment of "simulated" intruders, and "that communal vocalisations convey information about the size of the singing group" (Strong et al 2018 p206) (appendix C).

Strong et al (2018) studied the greater ani (*Crotophaga major*) (figure 2) in Panama. Typically a shared nest includes two or three pairs, and sometimes unpaired, non-reproductive helpers. Group sizes, then, are four to seven birds, and they all aggressively defend the nest site with loud communal chorusing displays (and by chasing intruders). Groups compete for high-quality nesting sites.

Data were available on a nesting population for the period 2007 to 2016. Most of the nests had two breeding pairs, with three or four or more pairs less common (around a quarter of the total). Complete data were obtained on 192 nests. Inter-group conflict was measured as destruction of all eggs in the nest by a neighbouring



(Drawing by Francois-Nicolas Martinet; from Special Collections of the University of Amsterdam; public domain)

Figure 2 - Greater ani.

group, and thus abandonment by the inhabitants. Eighteen nests (9.3% of the total) were, as Strong et al (2018) explained, "apparently destroyed by conspecifics outside

the social group. In all cases, eggs were found immediately underneath the nest during either the incubation period (N = 11) or the laying period (N = 7), after all of the females in the breeding group had started to lay. In the majority of cases (N = 14), field observers noted behavioural evidence of conflict between groups whose clutches were destroyed and their nearest neighbours (eg: chasing, alarm calling and communal displays) immediately before or immediately after the clutch was destroyed. Although we never directly observed clutch destruction in the field, we suspect that eggs were rolled out of the nest by extra-group individuals..." (p210).

Conflict was most likely to occur when two groups nested in close proximity in high-quality nesting sites. Group size did not influence the destruction cases - in six cases the aggressors were a smaller group, four cases larger, and in eight cases there was no difference in size between the aggressors and the defenders. The number of years that the group had previously nested at the site (tenure length) was significant. Data were only available on fifteen nests, and in nine cases "a previously established group destroyed the clutch of a group that had never before nested at the site; and in 2 of 15 cases, a longer-established group destroyed the clutch of a more recently established group" (Strong et al 2018 p211). In the remainder of cases, a longer-established group was ousted.

The researchers considered three possible explanations for the relationship between longer tenure length and success in inter-group conflict:

i) Asymmetrical expected pay-off - "a group that has nested on the same territory for several years might value that territory more highly than a newcomer group does, such that the established group has more to gain by evicting the newcomer (and more to lose if it is evicted)" (Strong et al 2018 p212).

ii) Longer tenure may represent older and more experienced birds, and these individuals "might be more likely, or better able, to attack neighbouring groups due to differences in individual knowledge, condition or perceived value of the nesting territory" (Strong et al 2018 p212).

iii) Unknown factors - "Groups that have nested on a territory for several years have, by definition, been able to maintain ownership of the territory and avoid

eviction. It is therefore possible that long-established groups are composed of higher-quality or higher-condition individuals, and that these unknown physiological or cognitive differences are responsible for both the stability and the competitive ability of long-established groups" (Strong et al 2018 p212).

In summary, for this social bird, relative group size was less important than tenure length in winning inter-group conflicts.

Only a small number of nesting events in the dataset had conflicts, and, to emphasise again, the researchers did not observe the removal of eggs by neighbours.

## **8. COLLECTIVE BEHAVIOUR AND TIMESCALES**

Living in groups is not necessarily the same as collective behaviour. This includes "the mechanisms that allow animals to maintain groups and transfer information, and how interactions between individuals give rise to group-level properties such as shape and spatial positioning within groups, group movement speed and direction, information transfer within groups, and collective decision making. These group-level properties are often emergent, as they are difficult to predict from the simple inter-individual interactions that drive them, which lack centralised or external control and are hence self-organised" (Ioannou and Laskowski 2023 p1).

Collective behaviour can be understood in terms of different time scales (Ioannou and Laskowski 2023):

i) Seconds or less than one second - eg: "how individuals interact within moving groups to achieve collective motion while maintaining group cohesion" (Ioannou and Laskowski 2023 p3), as in fish shoals, and bird flocks (ie: the response of an individual which is mirrored by others).

ii) Minutes, hours or days - eg: choice of direction for groups to move towards (ie: collective or quorum decision-making). Differences in knowledge or energy level between individuals means different influences within the group (eg: hungrier animals at the front of a moving group), and the emergence of leaders.

Deep learning algorithms are being used to study animals in collectives. Romero-Ferrero et al (2023) described an experiment with zebrafish in groups of fifteen where five of them had been trained to respond to

a light at a particular location for food. Twenty-two groups of fish were tested. The movement of the fish were video-recorded and an algorithm was trained to recognise individuals. It was found that as the trained fish responded to the light, the speed of that reaction influenced the behaviour of the neighbouring fish. "From the lens of decision-making, neighbour speed acts as confidence measure about where to go" (Romero-Ferrero et al 2023 p1).

iii) Over the lifespan - eg: the development of shoaling behaviour by fish at a certain age (eg: 17-19 days post-hatching in Spanish mackerel; Ioannou and Laskowski 2023) (appendix D).

iv) Evolutionary time - eg the appearance of collective behaviour in a species, but not in the ancestors.

"At the heart of any group decision are the conflicts of interest among individuals within the collective. When the preferences of individuals do not align, the collective must either resolve conflicts of interest through consensus (eg: to move in a specific direction or to change from one behavioural state to another) or choose not to act as a collective (e.g. group fission)" (Ogino et al 2023 p1). Factors influencing the resolution of conflict of interests can be divided into individual-level and group-level processes (Ogino et al 2023):

1. Individual-level processes - Individuals have different preferences about what the group should do, and these arise over different timescales:

a) Evolutionary - eg: local adaptation to predators. "If groups include individuals adapted to different local foraging regimes, these groups may experience higher consensus costs when making foraging decisions than groups who are locally adapted to share the same preferences" (Ogino et al 2023 p3).

Also sex differences. For example, male banded mongooses tend to be aggressive towards other groups, while females may mate with extra-group males. "Consequently, females are more often the initiators of intergroup encounters producing high consensus costs for males" (Ogino et al 2023 p3).

b) Developmental - eg: early life experiences and

later behaviours. For example, zebra finches reared in stressful environments are less selective about later social interactions.

c) Short-term - eg: individual nutritional state. "When foraging on a patch of resources, vulturine guineafowl (*Acryllium vulturinum*) that are excluded from the patch are motivated to continue searching for new food patches, causing the group to initiate movement and forcing those that are still feeding to leave the patch to follow the group" (Ogino et al 2023 p3).

2. Group-level processes - Group structure and composition can influence decisions:

a) Evolutionary-level - eg: mating system and social structure. For example, a conflict of interests in a kn-based group will be handled differently to a non-kin group.

b) Population-level - ie: changes in a group through births, deaths, immigration, and emigration impact decision-making.

c) Group dynamics - eg: dominants and subordinates. For instance, dominant vulturine guineafowl may exclude subordinates from food resources, and so subordinates leave the group.

There are so many factors that can influence the collective behaviour of the group, and involving different timescales. Ogino et al (2023) highlighted the problem of mismatched timescales in interpreting collective behaviour with data from nearly eight hundred tagged vulturine guineafowl in Kenya. The timescales of one month, two months, and eight months were compared in 2020-21.

Depending on the time period used, different social units were distinguished. For example, 98 groups using the one-month period compared to sixteen with an eight-month period. In summary, Ogino et al (2023) stated: "We show that applying different temporal definitions can produce different assignments of individuals into groups. These assignments can then have consequences when determining individuals' social history, and thus the conclusions we might draw on the impacts of the social environment on collective actions" (p1).

Sridhar et al (2023) made a similar point using data on schooling golden shiner fish, and flocking homing



pigeons from previous studies. The former (Davidson et al 2021) involved groups of ten or thirty golden shiner in laboratory tanks (*Notemigonus crysoleucas*), while GPS data on thirty homing pigeons (*Columba livia*) (Nagy et al 2013) were used. Three timescales of analysis were employed - less than fifteen seconds, greater than thirty seconds, and 60 seconds. The focus was upon interactions in the groups between pairs of individuals and leadership.

Different conclusions could be drawn depending on the timescale used. At less than fifteen seconds, in both groups, relative position of the individual animal was the strongest predictor of leadership. This suggested that "social influence is relatively linearly distributed across group members, ie: most or all individuals may exert some influence on group members" (Sridhar et al 2023 p6). With the longer timescales, individual differences became more important in terms of who is the leader (ie: the tendency to lead). This tendency may be linked to preferred flight speed in pigeons, say. So, "over longer timescales, inequality within the group grows, resulting in consistent inter-individual differences in leadership" (Sridhar et al 2023 p6).

Put simply, depending on the timescale used in analysis, different pictures of group behaviour will emerge - ie: that an individual can be a leader of the moving group (short timescale) or that certain individuals are more likely to lead (longer timescale).

The comparison of species was investigated further by Papadopoulou et al (2023) with shoals of stickleback fish (*Gasterosteus aculeatus*) in the laboratory, free-ranging flocks of homing pigeons, a free-ranging herd of goats (*Capra aegagrus hircus*) in Namibia, and a troop of wild chacma baboons (*Papio ursinus*) in South Africa. Collective motion events typical of each species were studied.

Similarities and differences between the four groups on a number of variables (eg: inter-neighbour distances; group shape; speed) were plotted (as a "swarm space"). The researchers concluded that "sampling a few seconds of collective motion (in our datasets 15 s) over a larger number of days (rather than collecting long trajectories over few days), may be a more advantageous way to capture the true characteristics of a species' collective motion" (Papadopoulou et al 2023 p6). The mechanisms of the collective motion were linked to "the specifics of locomotion" (Papadopoulou et al 2023 p6) (eg: the speed of acceleration and turning room to avoid collisions).

## 8.1. Group Development

Social groups change over their "lifespan", and Muratore and Garnier (2023) noted four "life stages":

i) Formation - The transition from solitary to group state, as in locusts. For example, this can be "triggered by tactile stimulation of the hindlegs acting as an indicator of a high density of individuals and leads locusts to undergo a hormonal change inducing social swarming behaviour" (Muratore and Garnier 2023 p3).

ii) Growth and development - This involves "the progressive transformations that the group undergoes on its way to its stable state..." (Muratore and Garnier 2023 p4). For example, "honeybees may sense worker density inside their colony via the collisions they experience with other workers. This mode of monitoring colony size triggers modifications of the workers' behaviours that can then lead to changes to comb structure" (Muratore and Garnier 2023 p4).

iii) Maturity (or "adulthood") - The group focuses here on maintaining its stability (or homeostasis) (eg: temperature and humidity regulation in the nest of social insects).

iv) Dissolution (or "death") - Some groups continue, but many groups are transient. Factors like food availability or parasites are relevant here. "For example, parasite infections in locusts can disrupt the gut bacteria responsible for producing pheromones leading to swarming behaviour" (Muratore and Garnier 2023 pp7-8).

## 8.2. Evolutionary Change

For complex social behaviours to evolve, there must be genes <sup>1</sup> that have changed over generations and under selection pressure. "The evolution of complex sociality is one of the major transitions whereby previously independent units unite to become mutually dependent components of a new level of individuality that represents a higher level of biological complexity - as a committed society. Examples of major transitions include the evolution of eukaryotes from prokaryotes, multi-

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<sup>1</sup> For example, a candidate gene for the shift from solitariness to aggregation has been isolated in the arched hooktip caterpillar (*Drepana arcuata*), which shows different behaviours and different stages of development (McLelland and Montgomery 2023).

cellularity from single-celled organisms, and animal societies from solitary-living individuals; the latter is epitomised by the most complex societies of insects (ants, termites, some bees and wasps), whose colonies are sometimes referred to as 'superorganisms'" (Sumner et al 2023 p2).

Key behaviours have evolved in such groups, including irreversibly committed division of labour (eg: queens and workers in insect colonies), and mutual commitment to the group (eg: specialist reproductive and non-reproductive individuals) (Sumner et al 2023).

Concentrating on social insects, Bourke (2011) proposed three stages in the evolutionary pathway from solitary individuals to superorganisms - (i) group formation, (ii) group maintenance, and (iii) "transformation into an obligate society composed of previously independent (related) individuals that are now incapable of living solitarily" (Sumner et al 2023 p3). West et al (2015) suggested two stages, from co-operative closely-related groups (stage 1) to "the transformation of such groups into a new 'higher-level' individual, composed of mutually dependent group members, who are usually related to each other (stage 2)" (Sumner et al 2023 p3). Other theories include twelve stages (Kirk 2005).

However many stages, there is a "point of no return", where individuals have evolved to be dependent on others. But is the process to this point incremental or large steps? The former idea suggests that small changes in genes gradually alter behaviour in the major ways needed, while the large steps approach might include changes to a whole segment of a chromosome at one time (and is sometimes called "punctuated evolution") (Sumner et al 2023).

It could be a combination of both processes, or different processes for different species, or at different times in evolutionary history.

McLelland and Montgomery (2023) felt that the interactions between larvae and host plants were key to the evolution of collective behaviour in caterpillars. Egg clustering, for example, is where multiple females lay on the same plant, and it is "likely that selection pressures favouring egg clustering provide the initial opportunity for collective behaviours to evolve" (p3) (eg: patchily distributed host plants).

But not all larvae that hatch from clustered eggs show collective behaviours, "suggesting additional, independent selection pressures must shape larval

behaviour and communication mechanisms. In part, these selection pressures relate to anti-predator defences" (McLelland and Montgomery 2023 p3).

Collective attacking of a leaf can better overcome plant defences, and so is another advantage of collective behaviour. "Group feeding can result in faster development for young larvae, allowing them to escape the vulnerable early instars more quickly" (McLelland and Montgomery 2023 p4).

### **8.3. Collective Learning**

"Collective learning" is "when collective performance at a task (ie: a measure integrating the behaviour of multiple individuals) changes consistently (usually improving members' fitness) when the group repeats a task (ie: increases its experience of it)" (Collet et al 2023 p2).

Here are three examples of collective learning (Collet et al 2023):

a) Temnothorax ants (Langridge et al 2004) - If the current nest is destroyed, scouts explore for a new site. "After finding a candidate new nest site, scouts will transport and/or lead other individuals to its location, until the whole colony has eventually 'decided' and settles in the new site" (Collet et al 2023 p3). Length of time for the colony to migrate can be measured, and, in experiments, it was shown to improve with repeated nest destructions. Researchers provided a choice of two sites to choose from.

b) Pigeons (Flack et al 2013) - "Across consecutive trials from a single release site, initially unknown to all birds, pigeon flocks refined and improved their collective routes to home, progressively approaching the straight line" (Collet et al 2023 p3).

c) Trinidadian guppy (Hansen et al 2021) - Shoals became faster and more efficient at finding food in a maze with two choices.

Collective learning is sometimes better than individual learning in the same situation. Collet et al (2023) offered three possible mechanisms of collective learning:

i) Individual learning occurs and this manifests as improved collective performance. "If all members' input improves, the collective performance should indeed improve, regardless of whether the collective decision emerges from some form of averaging (weighted or not) or from extracting a single solo contribution from among group members" (Collet et al 2023 pp4-5). One implication is that more knowledgeable individuals will become leaders.

ii) Individual members learn about other members and improved collective performance comes from these "better" interactions (eg: trust).

iii) Individuals learned to adjust their behaviour to the collective goal.

Note that there is "maladaptive learning" where experience leads to fitness disadvantages (Collet et al 2023). Also collective learning is not inevitable. It may not occur because "(a) the individual cognitive processing of information may be more challenging when several individuals, rather than only a single individual, contribute to a task; (b) what individual members learn and/or know does not necessarily influence the collective decision; (c) conditions for the emergence of collective learning need to be evolutionarily stable strategies, successfully traded off against other biological functions, to persist across generations" (Collet et al 2023 p9).

#### **8.4. Inter-group Co-operation**

Animal groups tend to be competitive or aggression towards others, "or at best avoid and tolerate other groups" (Rodrigues et al 2023 p1), but occasionally there is inter-group co-operation. Why would this latter behaviour evolve?

Rodrigues et al (2023) outlined two potential drivers: (i) "overriding threats from predators, competitors or adverse conditions" (p1) (ie: defence against threat), and (ii) temporary asymmetries between the groups in terms of resources (ie: "resource transfer").

Using mathematical modelling, Rodrigues et al (2023) found that localised dispersal was a key variable in the evolution of inter-group co-operation. This is where young adults leave their natal group and join another

group. If it is local, then the groups will contain genetically related members, and so co-operation is beneficial over aggression. "However, the evolution of these intergroup relationships may have significant ecological impacts, and this feedback may alter the ecological conditions that favour its own evolution. These results show that the evolution of intergroup co-operation is favoured by a specific set of conditions, and may not be evolutionarily stable" (Rodrigues et al 2023 p1).

## **9. MIXED SPECIES GROUPS**

Mixed species groups (MSGs) and aggregations include flocks of up to sixty species of birds, mixed herds of mammals on the African plains, and schooling fishes (Carlson et al 2023).

Key issues in the study of such groupings include (Carlson et al 2023):

- i) The species mix and composition of the group.
- ii) The spatial organisation of these groups (ie: how physically close individuals get).
- iii) Are some species leaders in moving and others followers?
- iv) The synchronising of behaviours.
- v) The impact of predators on the group. "Does predation pressure increase group formation? Do group participants share the same level of vulnerability to the same predators or does this vary across species? Are some species in these groups preferred by predators and therefore each species benefits differently in both degree and type of benefits they receive in the group?" (Carlson et al 2023 p2).
- vi) The flow of information through the group.
- vii) The effect of competition on the group structure.
- viii) The influence of the environment on group structure.

Synchronised behaviours, where "individuals perform Psychology Miscellany No. 186; July 2023; ISSN: 1754-2200; Kevin Brewer

the same activity while in the same location" (Daoudi-Simison et al 2023 p1), is a foundation of group cohesion. But it is not easy to study in mixed groups because "while an individual may be behaving synchrony with some members of its group, it will be asynchronous with others" (Daoudi-Simison et al 2023 p2).

Daoudi-Simison et al (2023) provided data on capuchins and squirrel monkeys at a zoo in Scotland. Point sampling was used, where an individual's behaviour was recorded at a point in time before moving on to the next individual. Five behaviours were scored - vigilance, foraging, locomotion, resting, and playing. Overall, behaviour synchrony was calculated at 40% (ie: total number of individuals engaged in the same behaviour at the same point of time). However, the within-species synchrony was significantly more than chance with the squirrel monkeys more synchronised than the capuchins.

This was a systematic observation based on the controlled nature of the zoo environment. "While no data are available to specifically answer whether capuchins and squirrel monkeys are synchronised in the wild, observational research has found that these groups often perform similar behaviours in the same locations. They have been frequently observed travelling and foraging together, with both species typically engaging in more foraging and less vigilant behaviour in the presence of the other than when in single-species groups" (Daoudi-Simison et al 2023 p2).

Using MSGs of birds, Kimball et al (2023) argued that the species within the group will show trait matching which will create differences to other members of the species not part of the MSG. For example, mixed-species flocks "often resemble each other in plumage" (Kimball et al 2023 p2). Such mimicry may facilitate communication, reduce aggression for subordinate birds, lower the risk of sticking out to predators, or smaller species benefit as larger birds could repel predators (Kimball et al 2023).

One of the advantages of group living is more eyes to spot predators and give alarm calls. Krama et al (2023) reported a case of selective alarm calling by birds in wintering single and mixed flocks of crested tits (*Lophophanes cristatus*) and willow tits (*Poecile montanus*).

Data came from observations in Norway over twenty years of twenty-five mixed species groups. Models of predators were used to elicit alarm calls at the

beginning of the wintering season (September-October), in the middle (December), and at the end (March). There was evidence of selective alarm calling depending on the time in the wintering season. It was found that "juvenile male crested tits begin withholding predator detection information (and shared vigilance) towards dominant male adults significantly earlier in the winter than dominant males begin withholding the same from juvenile males" (Krama et al 2023 p4). The individuals in these groups were non-kin. Dominance and territory ownership during the breeding season are important. The researchers suggested that "the mid-winter reduction of juvenile alarms could increase the likelihood of successful predator attacks on adults, increasing the chances for juveniles to replace adults and acquire their territories" (Krama et al 2023 p1). This was the case when male crested tits were in groups of their own species, but, in MSGs with willow tits, alarm calling did not change throughout the season. So, behaviour in a MSG was different to a single species group.

Environmental conditions can influence the tendency to flock in birds. Talking in reference to the Andes, Montano-Centellas et al (2023) observed that species inhabiting higher elevations (ie: harsher environments) have to deal with lower temperatures, which increases foraging and reducing vigilance, "two behaviours thought to promote flocking activity. Low temperatures can also reduce the activity and detectability of arthropod prey, further prompting birds to join flocks and increasing flocking propensity" (p2). The "open-membership hypothesis" proposes that "in harsher and structurally simplified environments, inter-specific flocking interactions are expected to be numerous and weak (ie: reduced flock structure as species join and leave independently) and flocking aggregations are expected to be less exclusive (ie: fewer preferred or avoided species associations, leading to a lack of clear flock subtypes). Consequently, flocks in harsher environments are expected to be more open and dynamic..." (Montano-Centellas et al 2023 p2). Flocks at lower elevations will be the opposite.

Montano-Centellas et al (2023) studied this idea with published and unpublished data from over 3600 flocks studied in the Andes between 1976 and 2019. The variables were elevation, human disturbance, and forest cover. Support was found for the open-membership hypothesis, suggesting opportunistic and unstructured flocking of species in harsher environments.



## 9.1. Moving Into New Areas

The "equilibrium theory of island biogeography" (ETIB) (MacArthur and Wilson 1967) explains the existence and extinction of a species on an island primarily through the island size. "A major tenet of ETIB is that increasing island area lowers extinction rates (ie: the area effect) as larger islands will have more resources, which lowers competition among species and allows larger population sizes" (Martinez et al 2023 p1).

Martinez et al (2023) investigated MSGs and ETIB with bird communities on islands in the Thousand Island Lake, Zhejiang Province, China. Annual data from thirty-six study islands from 2007 to 2016 were analysed for bird species, and more detailed surveys from periods in 2017, 2020, and 2021 for flock types. Twenty species were classified as never using MSGs, and 26 species as participants in MSGs.

Flocking propensity (ie: participation in a MSG) was found to predict successful colonisation of an island and lower extinction rate. In other words, flocking with other species was better for survival on a particular island than being in a single-species group in the main. Note that island size was also important as the ETIB predicted.

Martinez et al (2023) offered some possible reasons for the findings, including:

a) Newly arriving birds join an already-existing MSG.

b) General advantages of flocking (eg: dilution of individual predator risk).

c) Individuals of different species compete less directly because of different niches (eg: specific prey eaten).

d) Mutualistic benefits (eg: "mixed-species flocks might create niches for birds that capture insects beaten into the air by other species' gleaning activities"; Martinez et al 2023 p6).

More generally, invasive species could increase their chance of survival and establishment by joining groups of native species. "Most non-native species introductions fail to establish, possibly due to the shortage of conspecific individuals to perform vital tasks that require a group, such as avoiding predators or

finding mates" (Camacho-Cervantes et al 2023 p1).

There is a threshold of population size that is required for a non-native species to become established. In other words, the larger the initial population, the more likely the species will survive. This is known as the "Allee effect". MSGs could act as the population size threshold in some ways for the invading species. There is some irony here because invasive species could eventually replace the natives.

Camacho-Cervantes et al (2023) performed a literature review on positive interactions between native and non-native animals in terms of grouping together. Nineteen studies producing experimental or observational data were found, of which thirteen provided "evidence of non-native animal species deriving benefits from heterospecific sociability with natives" (Camacho-Cervantes et al 2023 p3). There were eight species studied, with the most common being freshwater fish, but snails, birds, mussels, and lizards.

The benefits can be classified as:

a) Sociability - eg: freshwater fish and general advantages of large group living.

b) Growth - eg: invasive freshwater snails and fish in MSGs had an increase in body size.

c) Transmission of information on food - eg: increased foraging success and efficiency.

d) Predator avoidance - eg: non-native mussels and parakeets.

e) Boldness and exploration - eg: being part of a group encourages exploratory behaviour that individuals may not be able to do.

Invasive species that join MSGs appear to gain group advantages in the early stages of their invasion (ie: prior to establishment and spread) (table 1). Note that four main stages of invasion have been distinguished - transport, introduction, establishment, and spread, and two main barriers - survival, and reproduction (Camacho-Cervantes et al 2023).

More studies are needed, including the benefits for native species of having non-natives in their MSGs (Camacho-Cervantes et al 2023).

- Transmission of information - food availability; shelter; predators
- Foraging - location of food; reduced time spent foraging
- Boldness - exploratory behaviour; dispersion
- Predators - grouping and dilution effect; alarm calls; distraction

(After Camacho-Cervantes et al 2023 figure 3)

Table 1 - Particular advantages of MSGs for invasive species.

## **APPENDIX A - LEKS**

Three main sexual selection hypotheses have been proposed for the evolution of lekking (DuVal et al 2018)<sup>2</sup>:

i) "Hotspot" - The idea is that "males settle in areas of high female traffic, either because females are common in those areas or because of shared habitat preferences, resulting in dense clusters of males in areas where there are also many females" (DuVal et al 2018 p216). This is "hit or miss", so the quality of males does not influence success, rather the number of females.

ii) "Hotshot" (or "spatial spillover") - More inferior males cluster around the most successful males in order to intercept females on the way to the "winners". This hypothesis predicts that inferior males that display near "winners" will be more successful.

iii) Female preference - Females are more likely to visit sites of male aggregation. This hypothesis predicts that lekking benefits the best quality males only.

DuVal et al (2018) studied the lance-tailed manakin (*Chiroxiphia lanceolata*), where a dominant alpha male displays and sings duets with a subordinate beta male (who does not mate usually). Data were collected from 2009 to 2013 in Panama (which included twelve video-monitored display sites in 2013).

The geographic centrality of the male in the lek did not influence female visits, but alpha males who

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<sup>2</sup> Other theories include indirect fitness, "black hole", and signal propagation (DuVal et al 2018).  
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displayed closer to other alpha males received more visits. "However, only males with many years in the alpha role had higher genetic reproductive success when they were close to other males" (DuVal et al 2018 p221).

## **APPENDIX B - INDEX SIGNALS**

Honest signals, like big antlers as a sign of large body size, are known as "index signals" (Maynard Smith and Harper 2003).

An interesting example is red colouration in birds <sup>3</sup>. This is produced by a particular biochemical process in the body (involving redox enzymatic reactions), and is a signal of "the bearer quality in an unfalsifiable way" (Fernandez-Eslava et al 2022 p2). The red colouration has been linked to "flying effort" because captive birds with red plumage moult to another colour (eg: male common crossbills). In other words, male red plumage signals a "flying metabolism", which is a desirable quality for females (Fernandez-Eslava et al 2022).

Fernandez-Eslava et al (2022) clipped the wings of a number of adult male common crossbills (*Loxia curvirostra*) to impact flying ability in their experiment. It was found that "male crossbills with experimentally impaired flying capacity and, probably, obligated to alter their metabolism were able to produce redder feathers than controls" (p5). So, male red plumage could be an honest signal of "the intrinsic quality of the bearer in terms of cell metabolism... [or] it could also reveal a general phenotypic profile, including the flying capacity and other correlated traits linked to fitness" (Fernandez-Eslava et al 2022 p7).

In other bird species, advantages have been observed in individuals with red colouration, including leaving earlier for migration (golden-crowned kinglets), and being better at avoiding predators (house finches) (Fernandez-Eslava et al 2022).

## **APPENDIX C - USE OF PLAYBACK**

Animals that live in low densities can be studied with scent-baited camera-traps, and autonomous audio recorders. These are forms of passive observation,

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<sup>3</sup> Bird colouration has to be seen in the context of bird colour vision (ie: how birds see the world and themselves). Birds have tetrachromatic vision, based on four retinal colour cone types, which allows them to see ultraviolet/violet wavelengths, red, green, and blue (Venable et al 2022).

whereas playback allows more active research (eg: testing hypotheses). Playback is widely used with primates, birds, insects, carnivores, and anurans (Ferreira et al 2021).

Ferreira et al (2021) reported the first use of playback with the maned wolf (*Chrysocyon brachyurus*) (figure 3) in a national park in Brazil. Recordings of roar-barks, the main form of long-distance vocalisation, were used to stimulate the vocal activity. Recordings of two males and two females were played for sequences of 5-25 minutes at different times and in different places (in March 2017). Roar-barks by free-ranging maned wolves within ten minutes of the playback were classed as responses.



(Source: Marie van Dieren; public domain)

Figure 3 - Two maned wolves in Leipzig Zoo in 2018.

Vocal responses were recorded in four of 21 playback sessions. Camera-traps showed that the animals approached the playback speaker when responding. Thus, playback could be used to survey and monitor the maned wolf presence. "To monitor absolute population size", however, Ferreira et al (2021) explained, "we would also need more information, such as individual emission rate, estimates of caller distance, and/or vocal individual identification" (p86).

Ferreira et al (2021) commented: "The vocal response rate obtained (4/21 sessions) may seem low, but maned wolves are not highly vocally active..., occur in very

low densities..., and we did not know a priori if there were any animals on the region at that time" (p87).

Giving more time for a response, like one hour, could be better as "vocal activity and approaches may be delayed" (Ferreira et al 2021 p89).

## **APPENDIX D - AGEING INDIVIDUALS**

Does ageing influence the behaviour of individuals in the group? "Growing evidence suggests that older adults differ in their social behaviours and social relationships from young adults. One pattern that seems to be emerging across taxa is that older adults interact with fewer individuals than do younger adults, concentrating social relationships on close associates and kin. Given that social networks are an emergent feature of association rules between individuals, shifts in patterns of social behaviour with age might not only affect who ageing individuals associate with directly (ie: their direct connectedness), but could also affect higher-order network structure" (Siracusa et al 2023 p2).

Indirectly, the proportion of older individuals in the group can influence processes within the collective. For example, older adults transfer information and learning to younger members, so a group with few ageing individuals will be weaker here (Siracusa et al 2023).

In relation to this topic, Siracusa et al (2023) analysed data from nineteen networks of female rhesus macaques (*Macaca mulatta*) on the island of Cayo Santiago (off Puerto Rico). This is an island populated only by macaques. Observational data were collected regularly between 2010 and 2017.

Groups with more old individuals (ie: above eighteen years old) were not structured differently from groups with less old individuals, contrary to expectations. Overall, the macaques were less connected in some ways, but not others. For example, the strength of relationships to their close partners was stable over time, but "betweenness" (ie: connections to the wider social network) declined. Higher-ranking individuals, in particular, showed less influence in the group with age.

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