

WHY ANIMALS COME TOGETHER, WITH THE SPECIAL CASE OF MIXED-SPECIES BIRD FLOCKS

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ABSTRACT

Group living is a widespread, ubiquitous biological phenomenon in the animal kingdom that has attracted considerable attention in many different contexts. The availability of food and the presence of predators represent the two main factors believed to favor group life. In this review, major theories supporting grouping behavior in animals are explored, providing an explanation of animal grouping. This review is divided in two sections. First, major theories as well as potential mechanisms behind the benefit of grouping are described. Later, a special case on the widespread animal social system of mixed-species avian flocks is presented, exploring the available information in relation to the potential causes that bring birds together into this particular social aggregation.

KEYWORDS: group living; mixed-species bird flocks; feeding efficiency hypothesis; predator defense hypothesis.

¿POR QUÉ LOS ANIMALES SE AGRUPAN? EL CASO ESPECIAL DE BANDADAS MIXTAS DE AVES

RESUMEN

El comportamiento de agrupamiento es un fenómeno biológico global y ubicuo en el reino animal que ha atraído considerable atención en muchos contextos. Los dos factores principales que se cree favorecen la vida en grupo son la disponibilidad de alimento y la presencia de predadores. En esta revisión se exploraron las principales teorías publicadas en la literatura que tratan de dar explicación al comportamiento de agrupamiento en animales. Esta revisión se divide en dos secciones. Inicialmente, se describen las principales teorías así como los potenciales mecanismos asociados al beneficio de agruparse. Posteriormente, se presenta un caso especial en un sistema social animal llamado bandadas mixtas de especies de aves, explorando la información disponible en relación a las causas potenciales que hacen que las aves se asocien en esta particular agregación.

PALABRAS CLAVES: agrupamiento; bandadas mixtas de aves; hipótesis de eficiencia en la alimentación; hipótesis de defensa de depredadores.

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RESUMO

O comportamento de agrupamento é um fenómeno biológico global e ubícuo no reino animal que tem atraído considerável atenção em muitos contextos. Os dois factores principais que se crê favorecem a vida em grupo são a disponibilidade de alimento e a presença de predadores. Nesta revisão exploraram-se as principais teorias publicadas na literatura que tratam de dar explicação ao comportamento de agrupamento em animais. Esta revisão divide-se em duas secções. Inicialmente, descrevem-se as principais teorias bem como os potenciais mecanismos associados ao benefício de agrupar-se. Posteriormente, apresenta-se um caso especial num sistema social animal chamado bandadas mistas de espécies de aves, explorando a informação disponível em relação a causa-las potenciais que fazem que as aves se associem nesta particular agregação.

PALAVRAS-CÓDIGO: agrupamento; bandos mistos de espécies; eficiência alimentar hipótese; hipóteses de defesa predador.

INTRODUCTION: A DEFINITION OF GROUP

There are a number of different approaches to defining what an animal group is (Wilson 1975, Pitcher and Parrish 1993, Lee 1994). Wilson (1975) characterized a group as '*any set of organisms, belonging to the same species, that remains together for a period of time interacting with one another to a distinctly greater degree than with other conspecific*'. Lee (1994) stated that '*when two or more animals live together they constitute a social unit*'. Nevertheless, groups can be composed of one species (i.e. monospecific groups) or customarily composed of more than one species (i.e. heterospecific groups). Known heterospecific groups are restricted to three major taxa: birds, mammals, including primates and ungulates, and fishes (Morse, 1977).

There seem to be general agreement that a certain degree of proximity in time and space is an essential prerequisite for grouping (Krause and Ruxton, 2002). For example, Pitcher, Magurran and Allan (1983) observed that coordinated group behaviors were only possible in cyprinids fishes if the individuals stayed within at least four to five body lengths of each other. Animals must be close enough for continuous information exchange between them, but distance can vary considerably between different species (e.g. cetaceans are capable of communicating acoustically over long distances; Krause and Ruxton, 2002).

A further requirement for so-called social groups is that animals are brought together by social attraction. This means that individuals actively seek the proximity of each other instead of co-occurring in the same spot because of an attraction to the same environmental condition such as a localized food source or a rock for basking (Krause and Ruxton, 2002). Finally, another important point to consider is that the division of animal species into group-living and solitary ones is largely artificial. Many (if not most) species are intermediates that will be found in association with con- or heterospecifics at certain times but not always. Also, for many so-called group-living species the group size distribution can vary widely and usually will include many singletons (Krause and Ruxton, 2002).

Benefits of group formation: why animals come together

The grouping behavior of fish schools, swarms of invertebrates, bird flocks and mammalian herds is mainly attributed to antipredatory and alimentary functions (Krause and Ruxton 2002, Zoratto, Santucci and Alleva 2009). Nevertheless, other potential benefits of grouping besides avoiding predators and finding food are related to finding a mate, protection against climatic adversities, increase in movement efficiency, or the combination of two or more of these factors (Roberts, 1996; Krause and Ruxton, 2002; Zoratto, Santucci and Alleva, 2009).



ANTIPREDATOR BENEFITS OF GROUPING

The main theories that attempt to explain how animal aggregations provide protection from predation are the many-eyes theory, the risk-dilution effect, the selfish herd theory, the confusion effect and collective defense (Krause and Ruxton, 2002; Zoratto, Santucci and Alleva, 2009).

The many-eyes theory several studies have demonstrated that larger groups are more effective at detecting approaching predators, i.e. “many eyes see better than only one eye” (Powell, 1974; Siegfried and Underhill, 1975; Treherne and Foster, 1980; Godin, Classon and Abrahams, 1988; Cresswell, 1994; Zoratto, Santucci and Alleva, 2009). Consequently, individuals in bigger groups detect predators earlier in an attack, compared with those in smaller groups (Krause and Ruxton, 2002). For example, a study conducted in wild pigeons (*Columba palumbus*) and one of their main predators, the goshawk (*Accipiter gentilis*), has proved that in the case of solitary birds, the reaction distance (i.e. the distance at which the prey reacts to the predator's attack) is low and the predator's efficiency diminishes as the number of birds in the flock increases (Kenward, 1978). The author suggested that this was probably due to the fact that when the predator is still far, at least one bird member can sight it. Hence, an individual in a group need not detect a predator itself to be warned of an attack, so long as at least one of the other group members does and informs the others.

Changes in vigilance level with group size has been well documented both empirically (e.g. Roberts, 1996; Hunter and Skinner, 1998; Greenberg, 2000; Pomara, Cooper and Petit, 2003; Zoratto, Santucci and Alleva, 2009) and theoretically (Pulliam, 1973; Pulliam, Pike and Caraco, 1982; Parker and Hammerstein, 1985; Lima and Bednekoff, 1999). For example, vigilance strengthening can be observed in ostriches (*Strunio camelus*): when in group, each single subject spends less time checking the horizon to locate possible predators than an isolated subject (Roberts, 1996). Theoretical models usually consider that foragers alternate periods of “feeding”, in which the predator cannot be located, with periods of “scanning”, during which a predator can be located. In general, transmission of information

throughout the group about a detected threat increases as the group's size increases, improving the overall vigilance level (the percentage of time in which at least one bird is watching; Bertram, 1980; Treherne and Foster, 1980). In this way, each bird gets both more time to feed and better vigilance of a predator's approach, and individuals can decrease their personal commitment to vigilance without increasing their risk of failing to detect an attack (Zoratto, Santucci and Alleva, 2009).

However, prey benefit from group scanning only if information is passed on quickly (Krause and Ruxton, 2002). Webb (1982) reported that the delay between the escape-inducing stimulus and the escape itself is lower for a shoal of fish than for a single fish. This rapid information transfer is the so called “Trafalgar effect”: information travels faster if members of a group are closer to each other (Treherne and Foster, 1981; Krause and Ruxton, 2002).

Finally, it is important to consider how group-life benefits are not necessarily equally distributed among group members. For instance, in starling flocks feeding on the ground, birds at the edge of the group dedicate more time scanning than those in the centre (Jennings and Evans, 1980). These differences often reflect dominance order: older subjects, more expert or larger individuals generally take the best positions in the centre of the flock while feeding on the ground (Jennings and Evans, 1980; Vehrencamp, 1983).

Risk-dilution effect sometimes called the encounter-dilution effect, states that an animal in a group reduces its probability of being singled out by a predator (Foster and Treherne, 1981). The risk-dilution effect combines three distinct concepts in one: predator avoidance, the attack risk dilution and abatement. Predator avoidance can occur when the perceptual range of the predator is low, relative to the movement speeds of predator and prey, such that predators must search their environment for prey. At the same time, grouping decreases the possibility of running into predators, widening the time between following encounters with them (Fitzgibbon, 1990; Zoratto, Santucci and Alleva, 2009).

In the case of the attack risk dilution, if a predator has discovered a group of prey, but can capture only one of them, then the larger the group the lower the chance that a particular individual will be the one attacked, so

the possibility for a single subject to be the potential prey becomes lower (Turner and Pitcher, 1986). Indeed, the probability might be expected to decline inversely with group size (Uetz and Hieber, 1994; Krause and Ruxton, 2002).

Many studies show that grouping animals are subject to a lower per individual predational risk than solitary animals. For example, there is evidence from experiments by Foster and Treherne (1981) on fish foraging on insects on the water surface, and Godin (1986) who found that the number of attacks by a predatory fish on a group of prey was independent of group size. Similar results were obtained by Morgan and Colgan (1987) using approaches of a predatory fish to different sizes of prey shoals behind glass. In general, the authors interpreted their results as evidence for per capita predation risk to decline as $1/N$, N being the group size. This concept is appropriate if the three following hypotheses occur 1) increased probability of being targeted must not be proportional to group size; 2) the probabilities for a predator to catch a prey must not be influenced by group size and 3) the predator must catch only one prey at a time (Krause and Ruxton 2002). The $1/N$ rule assumes that each individual is equally likely to be the one attacked, a circumstance that will often not hold if predators preferentially target some types of individuals. Furthermore, there is some evidence that larger groups are more conspicuous to predators resulting in higher overall attack rates (Krause and Ruxton, 2002; Morrell and James, 2008; Zoratto, Santucci and Alleva, 2009).

Foster and Treherne (1981) tested the risk dilution hypothesis in sea-skaters (*Halobates robustus*). These insects, living in group on the water surface, are predated by fishes which grasp them from the underneath: thus, vigilance cannot increase with group size. Predator attack frequency did not change according to group size and, therefore, the reduction in attacks in relation to the increase in group size was argued to be exclusively due to the dilution effect.

Not all experiments have produced support for the $1/N$ rule. Watt, Nottingham and Young (1997) presented toad tadpoles on a floating clear platform to a predatory fish. They found that strike rate increased with group size, but sub-linearly, so that individuals in larger groups received proportionally fewer strikes. Fels,

Rhisiart and Vollrath (1995) offered groups of croutons to circling gulls and found that the 'survival' probability of an individual crouton increased with group size, although not as quickly as the $1/N$ rule would predict; this was because gulls were, in general, more likely to capture an individual from a larger group.

Finally, the third, distinct concept in the risk-dilution effect is the so called abatement effect. If a group of N individuals is N times more likely to be detected as a singleton, then dilution will be insufficient to overcome this disadvantage to grouping. Due to this, avoidance and dilution must be considered together. Turner and Pitcher's (1986) theoretical synthesis on avoidance and dilution made clear that avoidance and dilution should be studied in combination, as what they called the attack abatement effect. They argued that in circumstances where there is no advantage to group-living from either dilution or avoidance alone, an advantage can accrue from the two mechanisms working together. Wrona and Dixon (1991) used data on predation on the pupae of a stream-dwelling insect to apply statistical methods for separating and comparing the effects of encounter reduction and dilution. They found that larger groups were more likely to be attacked than smaller groups (the opposite of the avoidance argument) but that within an attacked group, the probability that a focal individual was attacked was less in larger groups (revealing a dilution effect). They suggested that the second effect dominates the first, and so there was an overall attack abatement effect.

A particular type of dilution effect is the so called "time dilution", which depends on temporal, and not only on spatial, synchrony. It is likely that the rate at which a predator can catch a prey will have some upper limit (e.g. because subduing a prey individual takes a finite time). Prey can take advantage of this constraint by synchronizing emergence, which reduces the risk to the individual compared with when they present themselves individually over a longer time period (Sweeney and Vannote, 1982; Krause and Ruxton, 2002). This is thought to explain the observation of clustered emergence of bats from roosts (Krause and Ruxton, 2002). It has also been suggested as an explanation for synchrony of emergence of adult insects such as mayflies (Sweeney and Vannote, 1982) and cicadas (Lloyd and Dybas, 1966; Simon, 1979). Sweeney



and Vannote (1982) provided empirical evidence that the percentage of adult mayflies caught by predators is inversely related to the total number of adults available that day. An alternative explanation for synchrony could be an enhanced ability to find mate, but these authors found that synchrony among parthenogenetic mayflies was equal to (or perhaps greater than) that of sexual species (Krause and Ruxton, 2002).

As a final point, another benefit arising from the risk-dilution effect is based on predator learning (Zoratto, Santucci and Alleva, 2009). This is the case of the monarch butterfly (*Danaus plexippus*) in their communal roosting sites. Monarchs are toxic and bitter-tasting, a known mechanism of defense against predators. During winter, some birds attack them; despite the greater visibility of these aggregations, the number of predated butterflies is inversely correlated to roost size, since birds that have tasted one of them, presumably will not predate the others (Calvert, Hedrick and Brower, 1979).

The Selfish Herd The 'selfish herd' theory has been attributed to Hamilton (1971). It states that the risk of predation to an individual is reduced if that individual places another individual between itself and the predator (i.e. subjects group together to shield themselves when a predator approaches). When many individuals behave in this way, an aggregation is the inevitable result and because the risk is least near the centre and greatest at the edge, there should be a strong competition to obtain the best spatial position. Individuals of high social status will tend to occupy the centre and subordinate individuals will be pushed to the edge. Therefore, an individual in a group will gain protection from the vulnerability of those around it (Krause and Ruxton, 2002).

In Adelie penguins (*Pygoscelis adeliae*), for example, birds tend to not dive into water containing predators first or last, and it has been observed that when a penguin dives, all other individuals immediately follow (Court, 1996). Moreover, in colonies of bluegill sunfish (*Lepomis macrochirus*), a strong competition exists for occupying the central position, which guarantees lower predatory pressure on nests by egg-predating snails and higher cooperation with other fishes in keeping these egg-predators away (Gross and MacMillan, 1981).

Empirical evidence of the selfish-herd theory can be obtained by determining whether predation rates are higher in peripheral areas, assuming that predators attack the first prey encountered (Zoratto, Santucci and Alleva, 2009). Many studies, mainly conducted on fish, have sought such empirical evidence to show that the periphery is the most dangerous area (Krause and Tegeger, 1994; Barber and Huntingford, 1996). A plausible explanation for this may be that predators attack the periphery in order to detach a portion of the group (Parrish, 1989). Nevertheless, explanations not strictly related to the selfish-herd theory also could be considered. It has been suggested, for example, that with fish the higher predation rates in the periphery could be caused by an active prey selection by the predator, which could prefer specific phenotypes (e.g. smaller or younger subjects) usually located in the school's periphery (Stankowich, 2003).

The confusion effect The confusion effect describes the reduced attack-to-kill ratio experienced by a predator resulting from an inability to single out and attack individual prey in a group (Krause and Ruxton, 2002). This creates a disorienting effect on predators when approaching a dense group of prey, forcing them to attack the peripheral area of the group (Neill and Cullen, 1974). Such a disorientation effect is due to the fact that it is very difficult to follow, spot and catch a prey which moves rapidly across the visual field together with many others similar preys. The predator, because of the confusion effect, catches its victims from the group's periphery; therefore subjects occupying the central positions of a flock, of a school or of a herd are more protected than those confined to the margins (Zoratto, Santucci and Alleva, 2009).

The confusion effect received theoretical support from the artificial neural network model of Krakauer (1995). He created a simulation of a neural net able to predict the confusion effect and made the following predictions: a) all group members benefit from this protection, b) there is an exponential decrease in predator success with increasing group size, but in a decelerating way, with each additional individual added to the group having less effect than the last, c) increased protection occurs following group compaction, and d) the confusion effect is most effective when all individuals are alike, with odd individuals suffering

disproportionately from predation. Empirical support for the confusion effect is limited, perhaps because the design of experiments that rule out other confounding factors is challenging (Krause and Ruxton 2002). Milinski (1977) found that sticklebacks preferred to attack straying water fleas in aggregations. Kenward (1978) showed a strong decrease in the percentage of goshawk attacks that were successful as pigeon flock size increased. However, he did not attribute this to the confusion effect, but rather to weaker birds tending to forage in smaller groups (away from competition) and smaller groups being less able to detect oncoming attacks. Landeau and Terborgh (1986) and Parrish (1993) found evidence to support the confusion-effect theory with fish, as well as Zoratto *et al.*, (2009) for starlings.

Upon detecting a large quantity of identical fish or birds, predators become confused and have difficulties in both selecting and attacking a definite target, giving the prey individuals a chance to escape the predator. In relation to starlings, for example, it has been observed that, in the proximity of a peregrine falcon, they form more compact flocks and carry out coordinated mass movements, with the flock turning into a single and polarized moving unit (Zoratto, Santucci and Alleva, 2009). This kind of reaction has been observed in several species of fish (Magurran and Pitcher, 1987; Brown, Poirier and Adrian, 2004; Ferrari *et al.*, 2005; Templeton and Shriner, 2005) and birds (Dekker, 1980; Lima, 1993). Pitcher and Parrish (1993) suggested that these coordinated movements are aimed at enhancing the confusion effect, for instance through complex evasive manoeuvres carried out by fish schools to escape a predator.

Neill and Cullen (1974) conducted a laboratory experiment where several confounding factors were controlled. They demonstrated that four aquatic predators (squid, cuttlefish, pike and perch) had a reduced success rate per attack when attacking prey fish in groups, rather than singly. Similarly, Treherne and Foster (1982) demonstrated that the probability of successful attacks by a fish predator decreased as group size of marine insects increased. Fels, Rhisiart and Vollrath (1995) directly tested the confusion effect, neatly avoiding many confounding factors and ethical problems by using croutons as prey. Groups of croutons were thrown in the air, and attacked by waiting gulls. No

evidence for a confusion effect was found; indeed, gulls did better against larger groups. One drawback to these experiments is their artificiality. Many large predators, like hyenas and cheetahs, tend to isolate their prey as a hunting strategy to avoid the confusion effect (Krause and Ruxton, 2002).

Even though the confusion effect reduces predatory success, predators are attracted by grouped prey and reasons for the development of this apparently unfavourable grouping are not clear (Zoratto, Santucci and Alleva, 2009). One possible explanation for that, in cases where predators actively select their prey, is that predators want to be able to choose their prey (for example, preferring easy prey individuals to hunt down; Zoratto, Santucci and Alleva, 2009). Another explanation is that prey groups represent a super-stimulus: several studies conducted, especially on fish, showed that several species of predators prefer to attack schools more than single subjects (Morgan and Godin, 1985; Botham *et al.*, 2005; Zoratto, Santucci and Alleva, 2009).

Collective defense collective defense represents another strategy providing important benefits for the group. Several examples have been reported for a variety of animal species, ranging from baboons to musk oxens (Zoratto, Santucci and Alleva, 2009). Also known as mobbing, this behavior has been extensively investigated, especially for many species of passerines (Curio, 1978). In many cases, species subjected to high predation pressure are not passive. By living in a group, they are better able to defend themselves from predators. For instance, in a colony of blackheaded gulls, nesting pairs attacked a carrion crow flying around their nest and, in densely populated colonies, many gulls join in collective attacks when the crow approaches beyond a certain distance. This collective behaviour results in lower egg predation by the crow (Kruuk, 1964). In very dense common guillemot colonies, reproductive success is higher than in sparse ones, also thanks to a more effective collective defense against nest predators (Birkhead, 1977).

As can be concluded from the above, some of these theories must not be considered mutually exclusive; several might instead work complementarily (Krause and Ruxton, 2002; Zoratto, Santucci and Alleva, 2009). For example, because of the confusion effect, the



falcon may tend to hunt subjects at the periphery of the flock, generally launching an attack by moving closer or through dives into the sides of the flock, until one or more members split off from it, accidentally or not. At the same time, members of the flock, as a predator approaches them, immediately form a very thick and compacted flock (Morrell and James, 2008) in which every member attempts to reach a "central" position, where an individual can make use of its conspecifics as a shield against the predator's attacks (The selfish herd theory; Zoratto *et al.*, 2009).

FORAGING BENEFITS OF GROUPING

Benefits for predators: group hunting Grouping can allow predators to capture prey types that would be too large, too agile or dangerous for a single individual (Bednarz, 1988; Gese, Rongstad and Mytton, 1988; Creel and Creel, 1995). Protective groupings may be broken up by the simultaneous assault of several predators, or prey fleeing from one individual may become more obvious to others or may flee into their path (Krause and Ruxton, 2002). Group hunting can involve complex behaviors where individuals adopt different mutually complementary roles and exercise temporary restraint of feeding behavior until prey have been rendered more vulnerable. Such behavior has been observed, for example, in yellowtail fish hunting shoaling fish, which are collected and driven into the shallows before attacking (Schmidt and Strand, 1982), and in Harris Hawks while conducting cooperative hunting (Dawson and Mannan, 1991). Hunting in groups can also provide access to defended food sources. Flocks of jackdaws (Corvidae) can secure food items from much larger crows that would dominate a single bird (Röell, 1978). Similarly, flocks of juvenile ravens can overcome the defense of a territorial mated pair of adults and gain access to a carcass (Heinrich and Marzluff, 1995).

Joining behavior or coarse-level local enhancement The behavior of other group members is a potential source of information to an individual searching for food. It seems clear, both empirically and theoretically, that individuals use information from the position and behavior of others in order to increase the frequency with which they can obtain

food from ephemeral, hard-to-find patches, and a forager or group of foragers may attract others to the site of their foraging (Krause and Ruxton, 2002).

Drent and Swierstra (1977) compared two different types of model geese flocks with different geese in different postures - head down grazing posture and head up alert posture - and they found that the second group attracted over twice as many geese flocks to land nearby. Hence, geese used information not just about the presence of conspecifics, but also on their apparent behaviour when deciding whether or not to join the group.

Theoretical models predict that joining a group will either have no effect or a negative effect on an individual's net mean foraging rate, but its real advantage occurs in reducing the variance in times between obtaining food (Ruxton, Hall and Gurney, 1995). Net mean foraging rate does not increase since such a joining behavior does not increase the ability of a set of individuals to discover new food patches (compared with the aggregate of the same number of individuals searching independently; Ruxton, Hall and Gurney, 1995). Net mean intake rate can go down because of interference at foraging sites, or because new food patches are found less quickly than would be predicted for an equivalent number of independent searchers, because aggregations of individuals tend to lead to overlap of their search areas (Krause and Ruxton, 2002).

In heterogeneous groups, it may occur that dominant individuals, that can obtain more than their fair share of the food, can exploit such a system to boost their mean reward rate, but when individuals are effectively identical, then mean reward rate will probably decrease (Krause and Ruxton, 2002). This is not to say that such behavior would be selectively disadvantageous, as an individual that did not join in a population of joiners would often do worse, whereas an individual that exploited the discoveries of others in a population of non-exploiters would often do better. The costs and benefits of such behaviors are frequency-dependent and so a game-theoretical approach to predicting their overall fitness would be appropriate (Krause and Ruxton, 2002; Ale and Brown, 2007).

OTHER BENEFITS OF GROUPING

Finding a mate: communal leks Leks are communal mating grounds in which males display and females visit to mate, gaining no resources other than sperm from attending the lek (Wiley, 1991; Krause and Ruxton, 2002; Young *et al.*, 2009). They occur in species where males are unable to monopolize females or the resource needed for breeding. The attraction of lekking to females is likely to be that lekking allows a female to choose between a large number of potential mates, and also allows effective assessment of individual male quality (Sutherland, 1996; Young *et al.*, 2009). In the case of benefits for males, the reasons are not as clear as for females. It has been suggested that if females are more attracted to larger leks and more likely to copulate on each visit, then the average number of copulations per male will increase with lek size (Krause and Ruxton, 2002). However, this has not been observed for all lekking species (Sutherland, 1996). Moreover, recent evidences for the bower-building cichlid fish showed that males decreased their foraging rate with lek size, implying a cost to males maintaining territories on larger leks (Young *et al.*, 2009). Although this argument has been framed in terms of leks, such mate choice considerations may also play a part in colony formation. If females preferentially chose males with nesting territories close to high quality individuals, this would allow them a greater chance of obtaining extra-pair fertilizations from the high quality neighbour (Wagner *et al.*, 2000). Under this hypothesis, there is a trade-off for these poorer quality males: although physical proximity to a high quality male may increase their chance of obtaining a mate, this is done at the cost of suffering a reduction in their probability of paternity (Krause and Ruxton, 2002).

Defense against parasites Mooring and Hart (1992) reviewed considerable empirical evidence both for abatement and selfish herd effects against parasites. Grouping may, however, also incur a cost from less mobile contact-spread parasites (Krause and Ruxton, 2002). This notion received support from Rubenstein and Hohmann (1989) who found that the numbers of biting flies on an individual decreased with herd size in feral horses, but infection with endoparasites increased. Duncan and Vigne (1979) also studying semi-wild horses of Camargue (*Equus ferus caballus*), found that they

group more frequently in summer, forming larger herds. In this season, because of the warmer temperatures, they are more exposed to ectoparasites, mainly horseflies (*Tabanus* spp.). According to the dilution effect, in larger herds the probability of being attacked by horseflies is lower than in smaller ones.

Likewise, Poulin and FitzGerald (1989) conducted laboratory experiments using a free-swimming blood-sucking crustacean ectoparasite, preying on stickleback fish. They found that the frequency with which the ectoparasite attacked increased with the density of fish in the tank, but the success of these attacks was unaffected by density. Overall, the increase in attack rate was less than linear and each individual fish was less at risk when in a larger group, consistent with an abatement effect. Finally, Coté and Poulin (1995) carried out a meta-analysis that showed that the intensity of infection by mobile parasites consistently declined with group size, and discussed many incidents when hosts responded to increase mobile parasite abundance by forming bigger groups.

Conserving heat and water Reducing heat loss and increasing protection from desiccation are important benefits of grouping (Krause and Ruxton, 2002). Animals can conserve heat by huddling together, because this will reduce the fraction of their surface area that is exposed to the colder surroundings. Assuming that the other individuals in the huddle are at the same temperature, no heat will be lost through the surfaces in contact between them, and this benefit should increase with group size (Vickery and Millar, 1984; Canals, Rosenmann and Bozinovic, 1989). Hence, huddling in groups reduces the exposed surface area (Canals, Rosenmann and Bozinovic, 1997). Another advantage to huddling in a confined space is that heat lost from the bodies can significantly increase the heat of the surrounding air, reducing heat loss (Vickery and Millar, 1984; Canals, Rosenmann and Bozinovic, 1989). The same will be true for water loss through raising the humidity (Krause and Ruxton, 2002).

Substantial energetic savings through grouping have been demonstrated in several bird (Putaala *et al.*, 1995, Ancel *et al.*, 1997, Boix-Hinzen and Lovegrove 1998) and mammal (Andrews and Belknap 1986, Bazin and MacArthur 1992) species, although the opposite has also been shown (e.g. Berteaux *et al.*, 1996).



Huddling not only benefits endotherms: some slugs are known to pack closely together with large areas of their flanks in contact, which has been shown to lead to reduced water loss due to evaporation (Cook, 1981). Clark and Faeth (1998) showed experimentally that butterfly eggs in larger clusters were more protected from desiccation. The shape of the cluster was also shown to be important. They suggested that such water loss considerations may explain why egg clustering is more common in arid areas than in moist ones. Klok and Chown (1999) also demonstrated that clustering in insect eggs or larvae was useful to maintain water balance or body temperature.

Reducing the energetic costs of movement The idea that an individual can reduce the amount of energy required to move at a given speed by placing itself behind others has been suggested by many theoretical studies and has received qualified empirical support (Krause and Ruxton, 2002). The spiny lobster (*Panulirus argus*) forms single file queues of over fifty individuals as they walk across the ocean floor in migrations (Bill and Herrnkind, 1976). These authors measured the force required to pull preserved specimens on a wire, and found that the force required to pull a line of individuals was considerably less than the sum of the forces required to pull an equivalent number of single individuals at the same speed.

Many fish swim as a group showing synchronized and polarized behavior, which is generally termed schooling (Pitcher, 1983). There is evidence that individual fish in a school not in the front can gain considerable energetic savings, compared with swimming alone (Weihs, 1973). Nevertheless, Abrahams and Colgan (1985, 1987) argued that the optimal arrangement from a hydrodynamic viewpoint is a poor one for anti-predator behavior, because it would not allow fish to maximize the likelihood of predator detection. They further claimed that increasing the predation risk caused groups of fish to reorganize themselves in a way that made the group less hydrodynamically efficient, but it was likely to reduce predation risk.

There is good evidence that a fish's tail beat frequency is related to its energetic expenditure during travel (Herskin and Steffensen, 1998), and several studies report that fish at the back of a school beat their

tails at a lower rate than those at the front (Zuyev and Belyayev, 1970; Fields, 1990; Herskin and Steffensen, 1998). Thus, in conclusion, it seems likely that fish are able, at least under some circumstances, to make hydrodynamic savings through schooling behavior (Krause and Ruxton, 2002).

In terms of air movement, it is well established that aircraft can save energy by flying in formation (Hummel, 1995). According to Lissaman and Shollenberger (1970), this principle may be transferrable to birds, and energy saving has been suggested as an explanation for flight formations of some large bird species, particularly during long distance migrations (Krause and Ruxton, 2002). It is thought that the wake patterns produced by smaller birds are too complex and variable for another bird to be able to fly in a position that would allow energetic savings. Hence it is unlikely that this energy saving mechanism applies to small passerines (Hummel, 1995). This view is strengthened by the argument of Higdon and Corrsin (1978) that improved flight efficiency is not an important factor in three-dimensional flocks, such as those displayed by roosting starlings.

Nevertheless, the theory for larger birds has been well developed (Higdon and Corrsin, 1978; Hummel, 1983; Hainsworth, 1987-1988), and the maximum saving is achieved when birds are in a staggered formation with their wing tips overlapping in the direction of flight, as would be achieved by a V-shaped formation. However, line formations also are common, and are typical of large birds such as waterfowl, where birds fly arranged in single lines, often joined together (Bajec and Heppner, 2009). Weimerskirch *et al.*, (2001) tested the theory that birds actually experience an energetic benefit from formation flight by determining that a pelican's heart rate was 14% lower when flying in a V-shaped group than when flying alone.

An alternative or complementary theory explaining group formation among migrating birds is related to communication of navigational information (Krause and Ruxton, 2002). This theory predicts that wing tip spacing and depth (perpendicular to the direction of travel) should be correlated within a species, as individuals attempt to keep the birds in front of them in the centre of their visual field (Gould and Heppner, 1974; Badgerow, 1988).

GROUPING BEHAVIOR AND MIXED-SPECIES BIRD FLOCKS: A SPECIAL CASE

Mixed-species associations are known to occur in a great variety of vertebrate taxa in the animal kingdom, being recognized in fish schools (Ehrlich and Ehrlich, 1973; Itzkowitz, 1974; Alevizon, 1976), ungulate herds (Fitzgibbon, 1990; Hunter and Skinner, 1998), primate troops (Gartlan and Struhsaker, 1972; Terborgh, 1990; Peres, 1992; Cords, 2000), cetaceans schools (Pilleri and Knuckey, 1969) and bird flocks (Moynihan, 1962; Terborgh, 1990; Sridhar, Beauchamp and Shanker, 2009). However, nowhere else in the animal kingdom is the phenomenon of mixed-species associations more widespread than it is in birds (Greenberg, 2000). Mixed-species associations of birds are considered roving groups of individuals comprised of at least two species searching for food together (*sensu* Morse, 1970; Sridhar, Beauchamp and Shanker, 2009). These flocks show large variation in size, permanence and strengths of association (Moynihan, 1962; Terborgh, 1990; Greenberg, 2000), and include many different species in different parts of the world, such as tits (Paridae), woodpeckers (Picidae) and nuthatches (Sittidae) in temperate areas; antwrens, antshrikes (Thamnophilidae), and tanagers (Thraupidae) in the Neotropics, and babblers (Timaliidae), drongos (Dicruridae) and minivets (Campephagidae) in the Palaeotropics (Sridhar, Beauchamp and Shanker, 2009). Mixed-species forest flocks contrast with flocks found in open habitats (e.g. blackbirds, shorebirds and finches) in their smaller and more consistent sizes, more regular membership, presence of a consistent flock home range, and participation by a small number of individuals of each species (Terborgh, 1990).

Principal models to explain participation in mixed-species bird flocks

When considering hypotheses about the benefits and costs of mixed flocking, it is critical to recall that the presence of species-typical foraging specialization is one of the main ways in which these flocks differ from single-species flocks. Mixed-species bird flocks, especially in the tropics, often contain resource specialists that hunt insects in particular strata or microsites, such as dead leaf curls, bark, dead or live twigs, or tree boles,

or attack prey in specialized ways (e.g. long-distance strikes, hanging and reaching; Greenberg, 2000).

Of the previously reviewed theories about grouping in the animal kingdom, two main non-exclusive hypotheses that can be extended to birds have been proposed to explain why these participate in mixed-species flocks: (1) improved foraging efficiency, formally known as the feeding efficiency hypothesis, and (2) reduced risk of predation, known as the predator defense hypothesis (Morse, 1977; Krebs and Davies, 1981; Powell, 1985; Sridhar, Beauchamp and Shanker, 2009).

Foraging benefits of participation in mixed-species avian flocks

Improve feeding could occur through feeding on insects flushed by other birds (Winterbottom, 1943; Kotagama and Goodale, 2004), avoiding previously exploited areas (Cody 1971, Beauchamp 2005), copying foraging locations (Krebs, 1973; Waite and Grubb, 1988), and optimal movement patterns (Cody, 1971; Greenberg, 2000).

Beating for insects and other active prey Birds in flocks may capture insects that the members of the flock, as a whole, flush during their movement (Winterbottom 1943, 1949; Kotagama and Goodale, 2004). Drongos, birds native to tropical Africa, habitually capture insects in flight. The high frequency with which they join heterospecific flocks and capture insects flushed by them suggests that they obtain an advantage in these groups (Winterbottom 1943, 1949). The tendency in North American flycatchers such as wood pewees to join chickadee flocks in late summer (Morse 1970) may have the same explanation (Morse, 1977). Munn and Terborgh (1979) and Munn (1985) found that the bird leader species of Amazonian flocks, *Thamnomanes* antshrikes in the understory and White-winged shrike-tanagers (*Lanio versicolor*) in the canopy, depend heavily upon prey flushed by or stolen from other flock members. Munn (1986) further suggested that the antshrikes use a deceptive alarm call to induce subordinate birds to drop prey, which are then kleptoparasitized. Similar “deceptive” use of alarm calls has been reported for tits (Moller 1988). This author found that during periods of inclement weather, great tits (*Parus major*) gave alarm



calls when no predators were seen by the human observer.

To obtain such an advantage it is necessary that some individuals capture more flushed insects when in a flock than when alone. Further, unless all members do so, beating cannot be the primary basis for flocking. Likewise, this explanation clearly could not hold for groups that feed on seeds or other nonmotile foods (Morse, 1977).

Avoidance of previously exploited areas Foraging competition is a probable cost of mixed flock participation (Greenberg, 2000). However, since interspecific competition may occur anyway, participation in flocks may be a way to monitor the resource use of potential competitors (Morse, 1970; Austin and Smith, 1972). If food is evenly distributed and the items are small, it would not pay to forage where another individual has just fed. By avoiding substrates or sites that have already been used by another species, birds in mixed-species flocks may actually enhance their foraging efficiency (Greenberg, 2000). Within the spatial configuration of a flock, individuals may be able to see the location of others and to avoid their feeding sites (Morse, 1977). Cody (1971) found that desert finch flocks moved in a way that minimized duplication of effort. These flocks were elliptical and traveled in the same direction of their long axis, so that in large groups many individuals were lined up behind each other. However, individuals at the rear of a flock periodically flew to the front, so that a constant “rolling” action occurred and spatial overlap was consequently minimized (Cody, 1971). Morse (1970) argued that this behavior seems unlikely to hold for other types of flocks. The movement of the chickadee flocks that he followed were roughly elliptical and moved in the direction of their long axis too, but individuals in those flocks were very widely spaced, occupied relatively small ranges, and did not employ any rolling movement like those detected by Cody (1971).

Copying foraging locations One commonly suggested potential benefit of flocking is learning where food is located from other flock members (Greenberg, 2000) and, in the case that food is hard to find yet markedly clumped, it might pay to join successful foragers (Morse, 1977). The pattern of movement of individual foragers could convey that information to others. If individuals move rapidly between the areas

in which they forage actively (moving from clump to clump), it might be advantageous either to join them or to copy their activities by foraging in the same types of areas (Krebs, 1973; Waite and Grubb, 1988). There is little field evidence that birds in mixed-species flocks learn about the distribution of food from other flock members, but experiments carried out by Krebs, MacRoberts and Cullen (1972) demonstrated that when food supplies were clumped within a relatively small experimental area, great tits (*Parus major*), came to feeding sites that were being used by other individuals. Later, Krebs (1973) duplicated these results with heterospecific groups of black-capped chickadees and chesnut-backed chickadees, and showed that these two generalist species might gain information on productive foraging sites from each other.

The possibility that tit species learn from each other in the wild is particularly interesting in light of the specialization that has been reported among conspecifics in a flock (Vanburskirk and Smith, 1989). Waite and Grubb (1988) showed evidence from aviary experiments that copying can occur in mixed-species flocks consisting of tits, woodpeckers and nuthatches. Their experiment showed that attendant species (woodpeckers and nuthatches) pay attention to the foraging success of the more generalized tit species, at least in a confined aviary situation. However, more empirical evidences and field data are required to determine the importance of copying behavior (Greenberg, 2000).

Optimal movement patterns Cody (1971) proposed that mixed finch flocks move through a range in such a way as to optimize the harvesting of resources with respect to their renewal. When resources were abundant, he found that flocks moved more rapidly, turned more frequently, and that the angles of flock turns were larger, which brought the flocks back to previously visited areas more frequently. In general, mixed flock movements are irregular and seemingly haphazard, with no tendency to avoid previously visited areas at regular intervals (Greenberg, 2000). Gaddis (1980) concluded that chickadee/titmouse-led flocks are irregular in their movement, with no clear pattern of speed or direction. In a particularly careful study of flock movements, Powell (1979) found that flock movement approximated a random walk with a bias toward forward motion, and

that a dominant feature of flock movement was related to territorial boundary interactions.

Antipredation benefits of participation in mixed-species flocks

Reduced predation risk of participation in mixed-species flocks can arise through the selfish-herd effect (reduced predation risk in relation to the position of other group members; Hamilton 1971), the dilution effect (reduced probability of being singled out by a predator; Foster and Treherne 1981), the encounter effect (reduced probability of being encountered by a predator; Inman and Krebs, 1987), the confusion effect (reduced ability of a predator to single out and attack individual prey; Neill and Cullen, 1974), and the 'many-eyes' effect (increased probability of a predator being detected; Pulliam, 1973).

A number of studies have examined the role of group vigilance within single-species flocks (Powell, 1974; Siegfried and Underhill, 1975), and interspecific changes in vigilance have been documented for simple mixed flock systems (Barnard and Thompson, 1985). Experiments with food supplementation show that in temperate forests, mixed flocks of chickadees and other species break up and form local aggregations with more aggressive interactions (Berner and Grubb, 1985), rejecting protection from predators as a sufficient cause for mixed-species flocking. Sullivan (1984) first carefully tested the vigilance hypothesis in forest flocks by examining video footage of foraging downy woodpeckers in and out of mixed flocks, and found that vigilance time was much reduced in this bark-searching insectivore when it associated with other species. The decreased need for vigilance by attendants can also be seen as a feeding advantage, as the downy woodpeckers in flocks spent more time foraging.

Additionally, Charnov and Krebs (1975) suggested that avian mixed-species flocks can create disturbance to predators mainly by the use of alarm calls of certain species. There is evidence that many animal species are able to recognize and use the information in the alarm calls of heterospecifics (Lea *et al.*, 2008). The nuclear species, with their well-developed and conspicuous vocalizations, may be particularly attractive sources of information on the presence of predators (Greenberg,

2000). Both Morse (1970) and Gaddis (1980) showed that individuals of two tit species consistently alarmed first and most vociferously, with a loud whistle, when accipiters attacked mixed flocks. The whistled alarm causes all flock members to freeze, thereby reducing the conspicuousness of both the individual and the overall flock. Interestingly, in relation to alarm calls, as the number of birds increases in a flock, not only did the probability of detection of a predator increase, but so did the incidence of "false" alarm calls given mistakenly when no predator is actually present. Thus, there is a cost in losing foraging time to responding to inappropriate alarms (Lima, 1995; Greenberg, 2000).

The predator defense hypothesis and the feeding efficiency hypothesis have been tested in a variety of studies, particularly in temperate zones, but the relative importance of each hypothesis in explaining mixed-species flock formation is still widely debated, and a consensus is far from being reached (Jullien and Clobert, 2000; Sridhar, Beauchamp and Shanker, 2009). Support for both foraging and antipredator explanations has been found in one study or another (Cimprich and Grubb, 1994; Dolby and Grubb, 1998; Thiollay and Jullien, 1998; Thiollay, 1999; Beauchamp, 2004), although recent experimental (Hart and Freed, 2005) and empirical (Jullien and Thiollay, 1998; Jullien and Clobert, 2000; Sridhar, Beauchamp and Shanker, 2009) information tended to favour the predation hypothesis as a more relevant explanation (but see Berner and Grubb, 1985).

Several authors (Lazarus, 1972; Morse, 1977; Krebs and Davies, 1981; Powell, 1985; Popp, 1988; Thiollay and Jullien, 1998; Greenberg, 2000; Sridhar, Beauchamp and Shanker, 2009) agree with the idea that these two major potential benefits of flocking need not be mutually exclusive: participation in flocks might allow birds to exploit the vigilance of other species, reduce their own time spent in vigilance and correspondingly increase foraging efficiency. Decline in individual vigilance as group size increases is a common pattern for many types of flocks throughout the world, regardless of the specific mechanism involved (e.g. Roberts, 1996; Hunter and Skinner, 1998; Greenberg, 2000; Pomara, Cooper and Petit, 2003; Sridhar, Beauchamp and Shanker, 2009; but see Beauchamp, 2003), and the functional explanation of the group size effect remains



unclear. Even though it is generally considered that group vigilance or the 'many eyes' hypothesis prevail, there are alternative possibilities through encounter, dilution or confusion effects that have also found strong theoretical and empirical evidence (e.g. Roberts, 1996; Greenberg, 2000). Furthermore, it is not necessary that all participants in flocks accrue benefits: certain species that are joined by other species might in fact suffer costs from being in flocks (Zamora, Hodar and Gomez, 1992; Cimprich and Grubb, 1994; Pomara, Cooper and Petit, 2003).

Mixed-species avian flocking has puzzled ornithologists for decades, and the fitness advantages of mixed-species flocking behavior are still only partially understood (Peron and Crochet, 2009). Jullien and Thiollay (1998) and Jullien and Clobert (2000) obtained results suggesting an enhanced survival in obligate flocking species in tropical communities (68.7 and 75%, respectively), while other studies have shown that individuals fed at higher rates in vs. out of mixed-species flocks (Herrera, 1979; Hino, 1998; Thomson and Ferguson, 2007; Sridhar, Beauchamp and Shanker, 2009; Muñoz and Colorado *in prep.*). Perhaps the most comprehensive study on mixed-species flocks was that carried out by Sridhar, Beauchamp and Shanker (2009), who presented evidences for both predation and feeding enhancement. Using a large scale comparative analysis of mixed-species flocks, they found evidence of an important role of predation in the evolution of the flocking behavior in terrestrial foraging birds; higher flocking tendencies associated with traits thought to influence vulnerability to predation such as small size, insectivory and arboreal foraging. Additionally, they found that foraging rates of species increased and vigilance rates decreased in mixed-species flocks, suggesting that by associating in flocks, birds are able to exploit the vigilance of the mixed-species flock and reduce their own vigilance time, in particular for those species that are vulnerable to predation.

The past decades have seen remarkable progress in understanding the grouping phenomenon. The various hypotheses may explain, at least in a substantial proportion of the cases, the potential benefits of grouping behavior in animals, in particular from a viewpoint of the prey species. However, empirical evidences as well as a general agreement between theory and observation on

the relative importance of each one of these ideas are still lacking. Information of this kind is needed in order to improve our understanding of the relative importance of predation avoidance and foraging efficiency in the evolution of grouping behavior.

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