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Communication

Why Do Birds False Alarm Flight?

Meredith Root-Bernstein

UMR Centre d'Écologie et des Sciences de la Conservation, CNRS, Muséum National d'Histoire Naturelle, 75005 Paris, France; meredith.root-bernstein@mnhn.fr

Simple Summary: Bird flocks often take flight suddenly, as though escaping from a predator, even though no predator is present. This is called "false alarm flighting". It happens so often that it is considered a problem that needs to be explained—surely, it is a significant waste of energy and a loss of potential foraging time. I propose that there is actually a benefit to false alarm flighting, which is that it allows birds in flocks to practice escaping. I present an argument that taking off very rapidly in the context of escape behaviour is much faster than normal take-off behaviour, depends on body weight, and needs to be learned. It can benefit from constant adjustment to flock-mates' sensitivities and take-off times, and adjustment to one's own current weight, which varies rapidly in birds. My "fire drill" hypothesis posits that because of these potential benefits, false alarm flighting is a kind of beneficial motor practice.

Abstract: False alarm flighting in avian flocks is common, and has been explained as a maladaptive information cascade. If false alarm flighting is maladaptive per se, then its frequency can only be explained by it being net adaptive in relation to some other benefit or equilibrium. However, I argue that natural selection cannot distinguish between false and true alarm flights that have similar energetic costs, opportunity costs, and outcomes. False alarm flighting cannot be maladaptive if natural selection cannot perceive the difference between true and false alarm flighting. Rather, the question to answer is what false and true alarm flighting both have in common that is adaptive per se. The fire drill hypothesis of alarm flighting posits that false alarm flights are an adaptive investment in practicing escape. The fire drill hypothesis predicts that all individuals can benefit from practicing escape, particularly juveniles. Flighting practice could improve recognition of and response time to alarm flighting signals, could compensate for inter-individual and within-day weight differences, and could aid the development of adaptive escape tactics. Mixed-age flocks with many juveniles are expected to false alarm flight more than adult flocks. Flocks that inhabit complex terrain should gain less from escape practice and should false alarm flight less. Behavioural ecology framings can be fruitfully complemented by other research traditions of learning and behaviour that are more focused on maturation and motor learning processes.

Keywords: information cascade; maladaptive; alarm flight; maturation; learning

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1. Introduction

Ground-foraging, ground-breeding, tree-breeding and mountain-breeding flocking avian species flight en masse as an anti-predation strategy. Coordinated aerial group movements reduce each individual's risk of being targeted during attack by a flying predator [1,2]. Flocks also frequently take flight as an apparent anti-predation reaction, when no predation threat is present [3–6]. As I will describe below in more detail, flocks of birds such as mourning doves (*Zenaida macroura*) and starlings (*Sturnus vulgaris*) can often be observed, while foraging, to suddenly fly up from the ground, either land immediately or circle for variable periods, and resettle in the same location, for no obvious reason. They may do this frequently and appear agitated. This type of abrupt, agitated flighting can also be observed in the presence of predators, in which case it is associated with anti-predation behavior. This can be distinguished behaviorally from taking flight for reasons unrelated to predation [7–9]. Flocks of the same species can be observed to take flight after a period of roosting or assembling, but the flock takes to the air more slowly, and although the behavior may involve landing and flighting several times, it also differs from the anti-predation flighting in that it leads to the flock flying away to land elsewhere. I will use the term "false alarm flighting" to refer to flocks taking flight as an anti-predation reaction in the absence of a predator. False alarm flighting in response to a false, low-quality, or misinterpreted cue has been explained as the result of maladaptive information cascades [10,11]. According to this hypothesis, the frequency of false alarm flighting in the absence of a predation threat is explained by birds acting on socially acquired information about what they interpret to be predation risk in a rapid cascade, without evaluating it. In fact, birds may be leaving the flock for reasons unrelated to predation threat. When birds flight based on false information about predation risk, they lose foraging time, expend energy, and gain nothing [5,10].

If such a common phenomenon is maladaptive, birds should attempt to compensate for the cost. For example, birds could take advantage of the range of alarm signals [12] to communicate degrees of certainty about predation risk. Birds have been identified as having calm or reactive personalities [4], meaning that individuals have constant tendencies to have low or high thresholds of sensitivity and response to certain cues, e.g., potential predation cues. Given these personality differences, if birds need to compensate for costs of maladaptive false alarm flighting, calm individuals should prefer to form separate flocks which would be expected to have lower false-alarm flighting rates. This is because reactive birds, as well as calm birds, will prefer to associate themselves with calm birds to lower the costs of false alarms, but the presence of reactive birds will simultaneously raise the false alarm rate, negating the benefits of being around calm birds. Alternatively, if possible, calm birds might identify and ignore reactive birds within mixed-personality flocks. Finally, flocks that have wasted time alarm flighting when no predator was present should compensate by either foraging more intensively, increasing intra-flock competition for food, or ignoring subsequent alarms. I am not aware of evidence for false alarm flight compensation. However, Lima [13] reports that for some alarm cues, birds scan the environment (in addition to conspecifics) before deciding whether to flight, thus using 'personal information', and in a sense compensating for incorrect information [4,14].

If or when birds do not compensate for or avoid maladaptive false alarm flights, another possibility is that the maladaptivity of false alarm flighting is, on average, compensated by the large adaptive benefits of alarm flighting correctly on other occasions, or by all the advantages of the capacity to copy information. In the first case, we would have to assume that individuals escape likely death with sufficient frequency to compensate for the energy wasted due to frequent false alarm flights. I am unaware of any calculations attempting to assess this tradeoff. In any case, simply arguing that the existence of frequent false alarm flighting means that it must actually be adaptive does not address the critical question of how the trade-off is modulated so that the cost always remains smaller than the benefit. In the second case, where we argue that the perceived costs of false alarm flighting must be compensated by the on-average-beneficial capacity to copy information, we assume that copying is an invariant capacity that cannot be modulated according to circumstances. As suggested already above [4,14,15], and further discussed below, informational copying and assessment in situations of flighting and predator response is modifiable by learning and maturation. Species can maintain the beneficial capacity to copy information, without being developmentally obliged to copy in all behavioral contexts. It remains unclear why species that benefit from the capacity to copy information would consistently use this capacity in a maladaptive way in the particularly important context of anti-predation response.

Finally, a key problem I have with arguments about the maladaptive nature of false alarm flighting is the logical problem of which flights are adaptively costly and which represent an investment. In a case where there was an actual predator that correctly elicited a true alarm flight, but the individual in question is not killed, the expenditure of energy and the lost foraging time of that particular individual bird would be the same as for a false alarm flight, as would be the outcome. Why, then, should one such flight be maladaptive and the other adaptive? Natural selection sees only outcomes (the bird is alive at time y), not conditional outcomes (the bird is alive given the real presence of a predator at time x), and not alternative hypothetical outcomes against which to calculate advantage (the bird would have been dead if it had not flighted at time x). The maladaptive and the adaptive flighting behavior look the same to natural selection when they have the same energetic and opportunity cost, and the same outcome. Thus, all arguments that false alarm flighting is maladaptive per se strike me as logically hard to accept. This is not a claim that no behavior can ever be maladaptive; it is a specific claim that, in this case, natural selection cannot distinguish between false alarm flighting and true alarm flighting in the vast majority of cases. The question therefore cannot be why does the maladaptive behavior of false alarm flighting exist, but in what way can alarm flighting (false and true) per se be adaptive? Since natural selection cannot generally distinguish false from true alarm flighting, false alarm flighting should be adaptive for a reason common to true alarm flighting.

In response to these considerations, I propose an alternative hypothesis: false-alarm flighting is adaptive because individuals gain valuable motor practice whether the flighting is in response to a real predator or false information about a predator. Indeed, practicing escape is best performed in the absence of predators. Here I develop this "fire drill" hypothesis and its key predictions.

2. Materials and Methods

The research for this hypothesis took place between 2005 and 2021. I made my first Google Scholar search in 2005, and the last final search was performed in December 2021. All searches were conducted in English, and no Boolean operators were used. The main search terms used were: "alarm", "flighting", "birds", "avian", "flock", "escape", "anti-predation", "vigilance", "trade-off", "foraging", "personality", "variation", "threshold", "body condition", "information", "copying", "intention movement", "pre-flight movements", "coordination," "alarm call", "predator cue", "predator recognition", "juvenile", "take-off velocity", "habitat", "motor learning", "practice", "maturation", "exercise" and "FID". Search terms were not predefined at the beginning of the project but developed through snow-balling, meaning that when reading one paper I would look up citations from the paper, or have an idea that led me to develop a new line of enquiry and thus new search terms. Broadly, citation selection criteria are related to choosing those papers that most clearly address and evaluate the points I am trying to argue. In total, I analyzed about 400 papers, out of which about 15% were usable for my purposes. This paper is not a review, either systematic or otherwise and I did not follow a standardized protocol, like the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines, to gather and assess evidence to generate the hypothesis I develop here.

3. Results

3.1. Practicing Escape Is Adaptive

Fire drills are events in which groups of people practice escaping from a building which may be on fire in order to make this process effective, efficient and rapid. In theory, people practicing are unable to determine whether the fire alarm is based on true or false information until after the event. Analogously, I would argue that practice responding to false alarms can also improve alarm flighting in bird flocks. Many species benefit from practicing escape [15–19]. Escape involves not only knowing alarms and predator cues, but also mastering a set of tactics and learning or maturing motor coordination and speed [13,20–22].

When bird flocks take flight in non-alarm circumstances, they coordinate taking off through intention movements and other preflight movements [7–9,23–26]. The process of coordination of motivational states and movements can take several minutes or more [8,22,24–26]. In the air, many avian species coordinate flight trajectories through a set of simple behavioral responses to their nearest neighbors in the flock [26,27]. Coordinating behaviors and flying tactics may undergo a process of calibration, maturation or learning, although this has been little studied [27].

When flighting in response to a potential predation risk, birds do not perform intention movements or other preflight movements [8,9,27]. If performed, these movements are rarely followed by flighting [12]. Potential predator cues, alarm calls, wing noises, or conspecific flying movements are cues that birds may respond to when taking flight to escape potential predators [9,12,15,28]. Alarm flights typically initiate and complete within a few seconds [4,6,15,26,29]. However, there can be significant variation in time for flocks to take flight, as well as in likelihood of taking flight [4,15]. Possible sources of this variation include flock size, spacing between individuals, perceived predation risk, nature of the threat, the energetic state of the flock, habitat characteristics, and inter-individual variation in take-off times [4,5,15,27].

Alarm flights involve more work (energy expenditure) than other flights [30], and individuals can differ significantly in take-off times or angles [31–33]. Juveniles often gain more weight than dominant adults, which can slow their take-off [33]. Smaller daily weight gains in adults have no effect on take-off velocity or angle [30,32,34]. Birds may expend more energy in order to maintain constant speeds under weight gain [34], to re-allocate muscle mass [35,36], or to exert more motor control and fly more efficiently when heavier. Motor control makes velocity and precision achievable with less physical work, and is developed through practice [37]. Thus, I predict that practicing alarm flighting could compensate, partially or completely, for differences in weight affecting take-off velocities.

Compensation for inefficient take-off should be adaptive. Birds that take off more slowly are thought to be at greater risk of predation [31,33,34]. Although juveniles may be forced into exposed foraging sites by dominant adults in mixed-age flocks, risking exposure to predators but escaping competition for food, juveniles in flocks without adults can have higher mortality [38–40]. Juvenile birds show different, potentially maladaptive, responses to alarm calls compared to adults, such as freezing in the open, or moving nervously in cover [41–44]. Juveniles may favor foraging over vigilance, thus gaining greater vigilance benefits from flocking with adults than with other juveniles [38,43,44]. Although some avian species form juvenile flocks (e.g., starlings [45]), I have not found any studies comparing their flighting behavior to mixed-age or adult flocks. If juveniles are initially less likely to observe predators, less likely to take flight when they hear an alarm, and likely to take off more slowly, then flighting practice should play an important role either in maturation or motor learning of escape responses.

In summary, motor practice of escape via flighting could help compensate for inter-individual and within-day weight differences, and could aid the development of adaptive escape responses.

3.2. Practicing Motor Aspects of Escape vs. Reducing False Information Use

Various models examine how birds in flocks should react to ambiguous information, or information of unclear quality [13,46,47]. These models posit that through various rules of thumb governing individual behavior, individuals can reduce the risks of misclassification or perceptual constraints in the context of copying of information or social learning. For example, individuals can adjust the thresholds at which they respond to predation threats depending on cues about predator behavior and experience with different predators or environmental conditions [47,48]. This is separate to, and compatible with, the fire drill hypothesis. In my view, both are needed. If birds in flocks are able to reduce their use of ambiguous or false information, and yet continue to false alarm flight at high rates that are difficult to explain, there must be *another reason* why they continue to false alarm flight. That is, if any or all of the models of reduction of copying false or misclassified information are accurate, then birds must *already* be reducing their copying of false information, yet they *continue to false alarm flight*. Either some conditions leading to false alarm flighting exceed their capacity to reduce false information copying, in which case it is maladaptive and we return to my objections in the Introduction, or there is a benefit to false alarm flighting itself.

I argue that this benefit is not related to the issue of whether information is of good quality or not. The fire drill hypothesis is *not* about learning to distinguish false from real alarm calls or threat cues. The benefit that the fire drill hypothesis argues for is located in the realm of the advantages of *motor practice*. Thus, we move from a behavioral ecology framing of the costs and advantages of false alarm flighting to an ethological one. These framings should be compatible (compare [49]), such that birds can reduce costs of false information in ways that have been treated by other authors [13,46,50], while also practicing motor skills.

3.3. The Fire Drill Hypothesis of False Alarm Flighting

I argue that false alarm flights in bird flocks are adaptive. Like foraging and vigilance, I predict that foraging and alarm flighting must be traded off according to the balance of factors such as hunger, perceived predation threat and habitat characteristics [51]. Although a given individual in a flock may prefer foraging to alarm flighting and may thus ignore some potential predation threats or alarms, other individuals may be less inclined to forage and more inclined to fly to safety (i.e., 'better safe than sorry' [3,4,13]). Two factors may prevent flocks from breaking up due to different individual preferences or motivational states. One is conformity: birds prefer to stay close to one another while performing similar activities, to dilute predation risk or for other reasons [8,23,24,26,27]. This may, in effect, raise the flighting threshold of nervous birds near less-nervous birds. Another factor is consensus: when enough birds take to the air, even birds with a higher threshold for response to flighting cues are likely to take off [7,23,26,52]. Both conformity of action and collective consensus should allow flocks to coordinate alarm flights. Interestingly, small flocks could be both more vigilant, with lower response thresholds, and have more difficulty arriving at majority consensus post alarm flighting [5,51]. Some studies [5] report, however, that flock size does not affect false alarm flighting rates. Unlike in the maladaptive information cascade hypothesis, I predict that there are circumstances (as will be discussed below) under which all birds will lower their response thresholds in order to alarm flight more. It is unlikely, however, that thresholds would be lowered so far that all flight cues would elicit flighting [15,51].

Practice is only valuable if it trains real predation threat escape behavior. Flying or taking flight when not stressed, not in escape mode, or not under time pressure is a very different behavioral experience, as I summarized in the Section 3.1. In animals in general, locomotion when not practicing or simulating (e.g., through play) escape behavior appears to have little direct transfer to anti-predation skills [21,53]. As I argue above, juveniles may have the most to gain from practice [44]. However, adults may also benefit from continuous practice, especially when forming new flocks, mixed-species flocks, or experiencing weight changes (e.g., during migration, gravidity), since these factors will affect their response times and thresholds. If we compare bird flocks to mammal social groups and herds, false alarm escape *locomotion* (though not necessarily false alarm *calls*) seems to be greater among birds (although I am not aware of any quantitative comparisons); might this reflect that mammal group composition is often more stable and weight fluctuations of individuals are less abrupt and dramatic than in flocking birds? If so, this would suggest that adult birds also benefit from constant practice. This raises interesting questions such as: which birds initiate alarm flights? Which birds ignore alarms or take offs? Does the number of false alarm flights decline with age (juvenile or adult), average experience in a habitat, or time of flock persistence? How do motivational states and habitat characteristics affect alarm flighting frequencies?

An important paper on terrestrial escape learning [21] predicts that young animals should show a phase of rapid, apparently pointless movements around their home range representing escape motor practice, that motor practice is less valuable and less invested in when the habitat has more refuges, and that animals can use practiced escape routes in complex terrain as a way of losing persistent predators. All of these predictions can be adapted to understand false alarm flighting in birds. Flocks with young birds should be more likely to alarm flight. Even if juveniles initiate alarm flighting less than adults, they should have lower response thresholds and thus tip the balance of consensus. In environments with many trees, shrubs, or rocks, flocks should alarm flight less [54]. Finally, complex aerial movements and coordinations may be the avian flock equivalent of escape routes in complex terrain, and are thus more likely to occur during real attacks than false alarms—though they also require a phase of practice, perhaps predominantly when birds are juveniles or when flocks are newly formed.

In addition to improving motor coordination, both adults and juveniles may benefit from the exercise element of false alarm flighting. Research on animal exercise, which looks at physiological aspects of motor activity, has shown that adult birds can also obtain some benefits from at least some regimes of repeated and energetically costly movement. Although an exercise benefit would not be specific to false alarm flighting alone, and does not really constitute an argument for why alarm flighting should occur (exercise can occur in many ways), it may explain the mechanisms by which some of the adaptive benefits discussed above occur. Most of the research on exercise in birds is concerned with long-distance migration, which is not directly relevant to escape flights and take-off, which, for example, use different energy sources [55]. Studies of non-migratory flight, such as take-off, escape, and foraging, suggest that some exercise regimes can reduce oxidative stress to the muscles, reduce energy expenditure, and lead to increased exercise capacity [56]. Regular practice of escape flight in budgerigars increased their speed and reduced oxidative damage to the muscles [57]. To my knowledge there are no studies of the exercise benefits of false alarm flighting in the wild, but I predict that these benefits can also be obtained from false alarm flighting.

The limits of the "fire drill" analogy need to be recognized. My point in giving the hypothesis this name is just to remind us that practicing escape is beneficial. While in human terms, a fire drill is organized by some leaders to benefit a group (or to reduce legal liability), we do not need to assume that the fire drill hypothesis as applied to false alarm flighting in birds is a group-selection argument, or requires a leader who organizes the practice activity for the group. If we do not need to make these assumptions for adaptive bird flock flighting behavior in general, then we do not need to make them to explain adaptive false alarm flighting.

4. Conclusions

In summary, if we assume that false alarm flights are maladaptive per se, we can only explain them by finding a way in which they actually are adaptive—for example, their apparent costs are actually lower than some broad benefit (e.g., the capacity for social learning), or their rate of occurrence is at an adaptive equilibrium with non-false alarm flights. If, as I think is more likely, neither individual birds nor natural selection can reliably detect which anti-predation behaviors were successful because there was a real threat that was reacted to appropriately, and which were successful because there was no real threat, how any of these cost-benefit calculations can be carried out in reality is unclear. I argue that since natural selection cannot actually distinguish false alarm flighting from true alarm flighting, both should be adaptive for a reason that they have in common.

The fire drill hypothesis of alarm flighting posits that false alarm flights (as well as true alarm flights for all the birds not at risk of being targeted by the predator) are an investment in practice. It predicts that all individuals can benefit from practicing escape, particularly juveniles. Thus, flocks with many juveniles should false alarm flight more than adult flocks. Newly formed flocks, especially new flocks that are weight-heterogenous, mixed-species, or contain migrating or gravid individuals, should also false alarm more. Flocks that inhabit complex terrain should gain less from escape practice and should false alarm flight less. Behavioral ecology framings can be fruitfully complemented by other research traditions of learning and behavior that are more focused on maturation and motor learning processes [21,38,49]. Since false alarm flighting intersects with many key areas of current research—for example, vigilance and perception of predation risk [58–60], or communication and group coordination [28,61]—re-evaluating it could have a wide-ranging impact.

This paper develops the fire drill hypothesis using traditional methods of creative thinking and reasoning. It is possible that despite my efforts to logically examine the issues, I have missed some papers that demonstrate a priori that the fire drill hypothesis must be false and is not interesting. Undoubtedly, I have given logical weight to some of the information included in my argument in a way disproportionate to the weighting it would be given based on reported sample sizes or effect sizes. Finally, my analytical thinking process is creative, idiosyncratic, contingent on my other research experiences, and cannot be reduced to an algorithm; it is thus not replicable. A more objective and repeatable method of evidence synthesis would be to conduct a systematic review and a meta-analysis. It remains unclear to me how novel hypotheses can be developed without thinking that creatively synthesizes selected ideas or evidence, but other researchers are more than welcome to recreate, validate, and justify the fire drill hypothesis using protocols of objective data synthesis. Experimental research testing the hypothesis and its predictions would also be welcome.

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