False Alarm Flight of Birds

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Bird flocks often take flight suddenly, as though escaping from a predator, even though no predator is present. This is called "false alarm flighting".

information cascade

maladaptive

alarm flight

learning

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 $\frac{[1][2]}{2}$. Flocks also frequently take flight as an apparent anti-predation reaction. when no predation threat is present [3][4][5][6]. As researchers 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][8][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. researchers 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].

In response to these considerations, an alternative hypothesis has been proposed: 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.

2. 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, researchers would argue that practice responding to false alarms can also improve alarm flighting in bird flocks. Many species benefit from practicing escape [12][13][14][15][16]. Escape involves not only knowing alarms and predator cues, but also mastering a set of tactics and learning or maturing motor coordination and speed [17][18][19][20].

When bird flocks take flight in non-alarm circumstances, they coordinate taking off through intention movements and other preflight movements [7][8][9][21][22][23][24]. The process of coordination of motivational states and movements can take several minutes or more [8][20][22][23][24]. In the air, many avian species coordinate flight trajectories through a set of simple behavioral responses to their nearest neighbors in the flock [24][25]. Coordinating behaviors and flying tactics may undergo a process of calibration, maturation or learning, although this has been little studied [25].

When flighting in response to a potential predation risk, birds do not perform intention movements or other preflight movements [8][9][25]. If performed, these movements are rarely followed by flighting [26]. 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][26][12][27]. Alarm flights typically initiate and complete within a few seconds [4][6][12][24] [28]. However, there can be significant variation in time for flocks to take flight, as well as in likelihood of taking flight [4][12]. 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][12][25].

Alarm flights involve more work (energy expenditure) than other flights [29], and individuals can differ significantly in take-off times or angles [30][31][32]. Juveniles often gain more weight than dominant adults, which can slow their take-off [32]. Smaller daily weight gains in adults have no effect on take-off velocity or angle [29][31][33]. Birds may expend more energy in order to maintain constant speeds under weight gain [33], to re-allocate muscle mass [34][35], 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 [36]. Thus, researchers 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 [30][32][33]. 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 [37][38][39]. Juvenile birds show different, potentially maladaptive, responses to alarm calls compared to adults, such as freezing in the open, or moving nervously in cover [40][41][42][43]. Juveniles may favor foraging over vigilance, thus gaining greater vigilance benefits from flocking with adults than with other juveniles [37] [42][43]. Although some avian species form juvenile flocks (e.g., starlings [44]), researchers 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. 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 [17][45][46]. 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 [46][47]. 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 researchers return to my objections in the Introduction, or there is a benefit to false alarm flighting itself.

Researchers 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, researchers 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 [48]), such that birds can reduce costs of false information in ways that have been treated by others [17][45][49], while also practicing motor skills.

4. The Fire Drill Hypothesis of False Alarm Flighting

The Fire Drill Hypothesis argues that false alarm flights in bird flocks are adaptive. Like foraging and vigilance, researchers 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 [50]. 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][17]). 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][21][22][24][25]. 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][21][24][51]. 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][50]. Some studies report, however, that flock size does not affect false alarm flighting rates. Unlike in the maladaptive information cascade hypothesis, researchers 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 [12][50].

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. 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 [19][52]. As researchers argue above, juveniles may have the most to gain from practice [43]. 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 researchers 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 researchers 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 [19] 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 [53]. 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.

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