# FLIGHT-INITIATION DISTANCE IN BIRDS IS DEPENDENT ON INTRUDER STARTING DISTANCE

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***Abstract:*** The distance at which animals move away from approaching threats (often quantified as flight-initiation distance [FID], or flush distance) has been used by behavioral ecologists to understand the economics of antipredator behavior. Wildlife managers often use FID when seeking to develop set-back distances to reduce human impacts on wildlife. Economic models of escape behavior predict that escape decisions will be dynamic and will be influenced by both the costs and benefits of remaining. In contrast, wildlife managers often aim to generate a single set-back distance for each species. While a number of factors are acknowledged to influence FID, the starting distance between the observer and the animal is typically ignored in FID studies. For 64 of 68 species of Australian birds, I found a significant positive relationship between starting distance and FID. This demonstrates that, as predicted by economic models, species generally assess risk dynamically and flush at a greater distance as starting distances increase. My finding is consistent with the idea that animals accrue an attentional cost for continued monitoring of an approaching predator. Researchers or managers aiming to quantify human impact using FID should use starting distance as a covariate.

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***Key words:*** Australia, flight-initiation distance, flush distance, human impacts, Tasmania.

Flight-initiation distance (Ydenberg and Dill 1986), also called "flush distance" (Holmes et al. 1993) and "escape flight distance" (Madsen and Fox 1995), is the distance at which an animal moves away from an approaching threat. Flight-initiation distance is studied for both theoretical and applied reasons. Behavioral ecologists view FID as an antipredator behavior that, like other behaviors, should be optimized. In the case of FID, animals should minimize the cost of escape by not moving away from predators until the cost of remaining exceeds the cost of escaping. Ydenberg and Dill (1986) formalized this logic in a simple graphical model that has been used to study optimal escape distance and optimal escape speed (e.g., Bonenfant and Kramer 1996). Briefly, Ydenberg and Dill (1986) suggested that the cost of remaining in a particular location could be viewed as a declining asymptotic function. If animals were minimizing escape costs, the optimal escape distance would be at the intersection of this function and an increasing function that plotted the cost of leaving. Because the cost of leaving could be influenced by a variety of factors (e.g., locomotion is costly, opportunity costs exist for leaving a particularly good foraging patch or terminating an important behavior such as mating, and movement may increase conspicuousness to predators), optimal escape distance will vary as a function of the cost-of-leaving curve. We therefore expect animals to dynamically vary their escape decisions based on their current assessment of risk (Ydenberg and Dill 1986). For instance, we know that animals adjust escape speed as a function of perceived risk: woodchucks (*Marmota monax*; Bonenfont and Kramer 1996) have larger FIDs, and woodchucks and golden marmots (*Marmota caudata aurea*) run faster when farther from refugia (Blumstein 1992, Bonenfont and Kramer 1996). Moreover, the observation that species habituate to human activities suggests that individual experience and perceptions of risk influence FID.

Flight-initiation distance often is studied by having humans walk (Burger and Gochfeld 1991) or drive watercraft (Rodgers and Smith 1995) toward individual animals. Wildlife managers use the distance at which animals move away from an approaching human (or humans in watercraft) as an index of disturbance to develop set-back distances (Rodgers and Smith 1995), thresholds beyond which humans should not approach to minimize the risk of disturbance. While a variety of factors such as time of day (Burger and Gochfeld 1991), time of year (Richardson and Miller 1997), and exposure to humans (Cooke 1980) influence FID, managers often aim to generate a single (conservative) distance to define the buffer zone. This is justified by the species-specific nature of FIDs (Blumstein et al. 2003), but care must be taken when estimating these parameters.

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particularly for those factors that influence the costs of remaining (i.e., not flushing).

The exact shape of the relationship between distance to a predator and the cost of remaining has important implications for both theoretical and applied studies. As presented, Ydenberg and Dill's (1986) model does not offer the theoretical justification for a single FID because we expect different situations to influence the cost of leaving, and an optimal escape distance will exist for any given cost of leaving.

I suggest that Ydenberg and Dill's (1986) simple model of the cost of remaining requires some modification, and I propose a more likely model (Fig. 1). Below some threshold distance ($D_{min}$) animals will always escape because they perceive a maximum risk from an approaching predator (Fig. 1, Zone I). While $D_{min}$ may be influenced by experience (e.g., habituated animals may be more tolerant of human approach), at some point all individuals will escape. Above this threshold, we expect a zone of trade-offs (Fig. 1, Zone II) where the relative costs and benefits of escape are optimized. At some point, a distance will exist ($D_{max}$) beyond which animals will not move away from an approaching predator (Fig. 1, Zone III). This could result from either animals not being able to detect an approaching predator or from animals not assessing predation risk beyond this distance. Experience may also influence $D_{max}$. Nonetheless, a threshold distance, such as $D_{max}$, underlies the logic that wildlife managers apply when developing set-back distances. In practice, estimating this distance may be difficult because of the large range of distances in which animals optimize escape decisions. I explored this distance in my study.

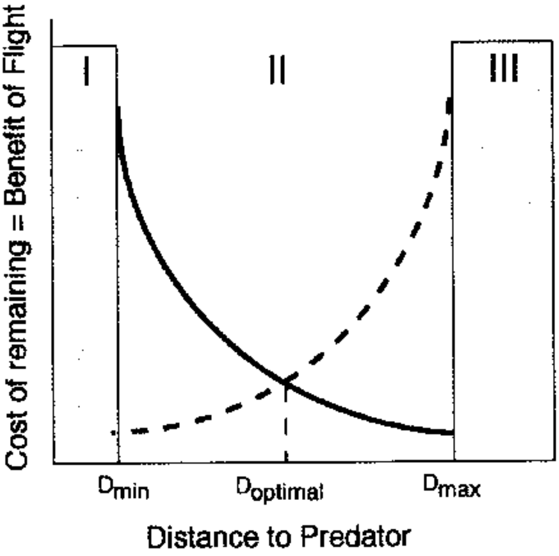

Fig. 1. Modification of Ydenberg and Dill (1986) economic model of flight initiation distance. The cost of remaining (which equals the benefit of flight; solid line) declines as the distance to an approaching predator increases. The cost of flight (dashed line) increases with distance to an approaching predator. The intersection between the cost of remaining function and the cost of flight function defines the cost-minimizing optimal flight initiation distance. The proposed modification suggests that species have 2 critical distances ($D_{min}$ and $D_{max}$) which create 3 zones: Zone I—animals will always respond to threats detected in this zone; Zone II—animals will optimize their escape dynamically as a function of the benefits and cost of flight; and Zone III—animals will not respond by fleeing from predatory stimuli beyond this distance.

Moreover, when researchers use FID as a means to assess human disturbance (e.g., Smit and Visser 1993, Lord et al. 2001), factors responsible for the dynamic nature of FID may confound interpretation of the main effect of human disturbance. One such factor may be the distance from which the observer begins walking toward the focal subject. An animal that detects an approaching potential predator has 3 options: (1) ignore the predator and continue current activity, (2) flee immediately, or (3) monitor the behavior of the predator while continuing current activity. The latter option is energetically costly and reduces the benefits associated with the animal's current activity. Thus, we might expect animals that detect a person at a greater distance might flee at a greater distance. If so, FIDs quantified either by fixing the starting distance or without knowledge of the starting distance may give biased estimates of both the mean and variance in FID. Practically, starting distance typically is ignored and assumed not to be important (but see Holmes et al. 1993, Lord et al. 2001). I used a large sample of Australian birds to demonstrate that starting distance generally influences FID and should thus be considered in future investigations.

## METHODS

To study the relationship between FID and starting distance, assistants and I identified individual birds and then walked directly toward them at a steady pace (approx 0.5 m/sec) while maintaining eye contact. Birds were first identified at a range of distances (Table 1). We focused on birds that were foraging or engaged in relaxed behaviors, such as preening or roosting. While we assumed that birds were relaxed when we started our experimental approaches, we are unable to determine whether they had already detected us. We did not approach highly vigilant

Table 1. The relationship between starting distance and flight-initiation distance (FID) for 68 species of birds in eastern Australia and Tasmania. Included are each species studied, the number of experimental approaches per species (*n*), the range of starting distances (Start range; given in m), the average and standard deviation of the FID for each species, and the results of a linear regression of starting distance on FID ($R^2$ and *P*-value).

| Latin name | Common name | Family | *n* | Start range | FID (SD) | $R^2$ | *P*-value |
|---|---|---|---|---|---|---|---|
| *Alectura lathami* | Australian brush-turkey | Megapodiidae | 27 | 8–95 | 12.0 (13.0) | 0.408 | <0.001 |
| *Anas castanea* | chestnut teal | Anatidae | 57 | 13–158 | 46.0 (21.4) | 0.672 | <0.001 |
| *Anas superciliosa* | Pacific black duck | Anatidae | 50 | 6–162 | 38.9 (29.0) | 0.756 | <0.001 |
| *Chenonetta jubata* | Australian wood duck | Anatidae | 45 | 7–160 | 25.5 (24.9) | 0.881 | <0.001 |
| *Phalacrocorax carbo* | great cormorant | Phalacrocoracidae | 36 | 15–115 | 32.3 (20.6) | 0.609 | <0.001 |
| *Phalacrocorax melanoleucos* | little pied cormorant | Phalacrocoracidae | 67 | 15–162 | 19.7 (14.3) | 0.275 | <0.001 |
| *Phalacrocorax sulcirostris* | little black cormorant | Phalacrocoracidae | 37 | 19–155 | 22.9 (15.5) | 0.3 | <0.001 |
| *Phalacrocorax varius* | pied cormorant | Phalacrocoracidae | 27 | 23–132 | 31.2 (18.0) | 0.169 | 0.033 |
| *Pelecanus conspicillatus* | Australian pelican | Pelecanidae | 66 | 15–300 | 32.6 (25.4) | 0.579 | <0.001 |
| *Egretta novaehollandiae* | white-faced heron | Ardeidae | 56 | 12–191 | 30.8 (20.2) | 0.137 | 0.005 |
| *Threskiornis molucca* | Australian white ibis | Threskiornithidae | 75 | 13–224 | 32.8 (20.4) | 0.204 | <0.001 |
| *Gallinula tenebrosa* | dusky moorhen | Rallidae | 37 | 9–59 | 14.8 (10.7) | 0.739 | <0.001 |
| *Porphyrio porphyrio* | purple swamphen | Rallidae | 68 | 9–186 | 34.5 (21.8) | 0.506 | <0.001 |
| *Arenaria interpres* | ruddy turnstone | Scolopacidae | 47 | 9–46 | 14.4 (6.5) | 0.045 | 0.155 |
| *Calidris ruficollis* | red-necked stint | Scolopacidae | 62 | 12–62 | 16.4 (8.7) | 0.306 | <0.001 |
| *Heteroscelus brevipes* | grey-tailed tattler | Scolopacidae | 48 | 9–164 | 17.3 (8.6) | 0.393 | <0.001 |
| *Limosa lapponica* | bar-tailed godwit | Scolopacidae | 196 | 11–227 | 22.1 (14.8) | 0.219 | <0.001 |
| *Numenius madagascariensis* | eastern curlew | Scolopacidae | 69 | 32–240 | 65.5 (41.6) | 0.464 | <0.001 |
| *Haematopus fuliginosus* | sooty oystercatcher | Haematopodidae | 62 | 24–128 | 30.5 (15.8) | 0.145 | 0.002 |
| *Haematopus longirostris* | pied oystercatcher | Haematopodidae | 48 | 39–329 | 37.9 (17.7) | 0.117 | 0.017 |
| *Himantopus himantopus* | black-winged stilt | Recurvirostridae | 65 | 22–152 | 38.8 (21.1) | 0.659 | <0.001 |
| *Elseyornis melanops* | black-fronted dotterel | Charadriidae | 44 | 12–68 | 23.1 (9.5) | 0.224 | 0.001 |
| *Vanellus miles* | masked lapwing | Charadriidae | 60 | 21–211 | 46.8 (30.5) | 0.387 | <0.001 |
| *Larus novaehollandiae* | silver gull | Laridae | 288 | 3–216 | 16.8 (12.1) | 0.113 | <0.001 |
| *Sterna bergii* | crested tern | Laridae | 68 | 10–178 | 17.3 (10.7) | 0.005 | 0.581 |
| *Ocyphaps lophotes* | crested pigeon | Columbidae | 31 | 8–56 | 12.6 (9.3) | 0.431 | <0.001 |
| *Streptopelia chinensis* | spotted turtle-dove | Columbidae | 52 | 5–62 | 12.7 (9.0) | 0.232 | <0.001 |
| *Cacatua galerita* | sulphur-crested cockatoo | Cacatuidae | 43 | 5–91 | 13.6 (11.8) | 0.549 | <0.001 |
| *Cacatua roseicapilla* | galah | Cacatuidae | 31 | 8–85 | 9.9 (6.3) | 0.155 | 0.031 |
| *Platycercus elegans* | crimson rosella | Psittacidae | 49 | 5–58 | 9.2 (7.8) | 0.47 | <0.001 |
| *Platycercus eximius* | eastern rosella | Psittacidae | 27 | 6–49 | 10.4 (6.6) | 0.181 | 0.030 |
| *Dacelo novaeguineae* | laughing kookaburra | Halcyonidae | 57 | 4–88 | 13.2 (13.0) | 0.433 | <0.001 |
| *Eurystomus orientalis* | dollarbird | Coraciidae | 32 | 8–137 | 21.9 (24.1) | 0.703 | <0.001 |
| *Malurus cyaneus* | superb fairy-wren | Maluridae | 95 | 2–31 | 6.4 (3.5) | 0.3 | <0.001 |
| *Malurus lamberti* | variegated fairy-wren | Maluridae | 39 | 3–29 | 4.3 (3.4) | 0.4 | <0.001 |
| *Acanthiza pusilla* | brown thornbill | Pardalotidae | 29 | 3–20 | 4.3 (3.4) | 0.289 | 0.003 |
| *Gerygone mouki* | brown gerygone | Pardalotidae | 35 | 4–16 | 3.6 (2.0) | 0.156 | 0.019 |
| *Sericornis citreogularis* | yellow-throated scrubwren | Pardalotidae | 49 | 3–33 | 5.6 (4.5) | 0.439 | <0.001 |
| *Sericornis frontalis* | white-browed scrubwren | Pardalotidae | 43 | 3–21 | 4.1 (2.5) | 0.381 | <0.001 |
| *Acanthorhynchus tenuirostris* | eastern spinebill | Meliphagidae | 42 | 4–19 | 4.8 (3.1) | 0.159 | 0.009 |
| *Anthochaera chrysoptera* | little wattlebird | Meliphagidae | 40 | 5–35 | 6.2 (3.5) | 0.133 | 0.021 |
| *Lichenostomus chrysops* | yellow-faced honeyeater | Meliphagidae | 31 | 4–22 | 4.7 (4.1) | 0.475 | <0.001 |
| *Manorina melanocephala* | noisy miner | Meliphagidae | 40 | 5–154 | 4.6 (4.4) | 0.017 | 0.426 |
| *Manorina melanophrys* | bell miner | Meliphagidae | 47 | 3–38 | 4.0 (3.2) | 0.304 | <0.001 |
| *Meliphaga lewinii* | Lewin's honeyeater | Meliphagidae | 45 | 4–70 | 7.6 (6.5) | 0.493 | <0.001 |
| *Philemon corniculatus* | noisy friarbird | Meliphagidae | 64 | 5–41 | 10.0 (5.9) | 0.245 | <0.001 |
| *Phylidonyris novaehollandidae* | New Holland honeyeater | Meliphagidae | 50 | 3–46 | 7.1 (4.6) | 0.262 | <0.001 |
| *Eopsaltria australis* | eastern yellow robin | Petroicidae | 84 | 3–45 | 9.4 (5.6) | 0.405 | <0.001 |
| *Heteromyias albispecularis* | grey-headed robin | Petroicidae | 26 | 4–57 | 9.2 (6.9) | 0.22 | 0.016 |
| *Psophodes olivaceus* | eastern whipbird | Cinclosomatidae | 55 | 5–29 | 5.8 (3.3) | 0.247 | <0.001 |
| *Grallina cyanoleuca* | magpie-lark | Dicruridae | 99 | 2–100 | 18.8 (10.6) | 0.436 | <0.001 |
| *Gymnorhina tibicen* | Australian magpie | Dicruridae | 95 | 3–66 | 10.5 (8.8) | 0.149 | <0.001 |
| *Rhipidura fuliginosa* | grey fantail | Dicruridae | 44 | 5–34 | 6.2 (4.4) | 0.347 | <0.001 |
| *Rhipidura leucophrys* | willie wagtail | Dicruridae | 54 | 5–82 | 11.5 (9.8) | 0.739 | <0.001 |
| *Coracina novaehollandiae* | black-faced cuckoo-shrike | Campephagidae | 26 | 14–100 | 19.8 (14.5) | 0.65 | <0.001 |
| *Oriolus sagittatus* | olive-backed oriole | Oriolidae | 35 | 3–52 | 10.2 (6.8) | 0.608 | <0.001 |
| *Strepera graculina* | pied currawong | Artamidae | 31 | 5–86 | 14.8 (14.5) | 0.457 | <0.001 |
| *Corvus coronoides* | Australian raven | Corvidae | 70 | 9–165 | 25.6 (22.6) | 0.704 | <0.001 |
| *Ptilonorhynchus violaceus* | satin bowerbird | Ptilonorhynchidae | 28 | 5–27 | 9.1 (5.4) | 0.432 | <0.001 |

*(continued on next page)*

Table 1. continued.

| Latin name | Common name | Family | *n* | Start range | FID (SD) | $R^2$ | *P*-value |
|---|---|---|---|---|---|---|---|
| *Anthus novaeseelandiae* | Richard's pipit | Motacillidae | 62 | 5–61 | 12.3 (5.2) | 0.122 | 0.005 |
| *Lonchura punctulata* | nutmeg mannikin | Passeridae | 42 | 5–41 | 11.1 (6.3) | 0.205 | 0.003 |
| *Neochmia temporalis* | red-browed finch | Passeridae | 68 | 5–46 | 7.1 (5.3) | 0.303 | <0.001 |
| *Hirundo neoxena* | welcome swallow | Hirundinidae | 36 | 7–104 | 10.9 (5.8) | 0.162 | 0.017 |
| *Cisticola exilis* | golden-headed cisticola | Sylviidae | 38 | 2–25 | 5.2 (3.1) | 0.505 | <0.001 |
| *Zosterops lateralis* | silvereye | Zosteropidae | 36 | 4–31 | 5.5 (3.9) | 0.417 | <0.001 |
| *Zoothera lunulata* | bassian thrush | Muscicapidae | 31 | 6–34 | 8.9 (3.1) | 0.026 | 0.387 |
| *Acridotheres tristis* | common myna | Sturnidae | 40 | 9–75 | 11.6 (9.4) | 0.633 | <0.001 |
| *Sturnus vulgaris* | common starling | Sturnidae | 30 | 10–60 | 14.0 (9.3) | 0.264 | 0.004 |

and obviously alarmed birds, nesting birds, or endangered species. To our knowledge, our experimental approaches did not harm the birds; most resumed their previous activity in a different location within 30 sec of initially moving (D. T. Blumstein, unpublished data).

I conducted my study in a variety of habitat types in eastern Australia and Tasmania. My assistants and I used a broad range of starting distances, both within and between species. All distances were measured in paces and converted to meters. We noted both the distance between the focal bird and observer when we started walking (starting distance) and the distance at which the focal bird moved away either on foot or by flight (FID). In most cases, flight was obvious, although shorebirds sometimes foraged by walking along the shoreline. In these species, we identified FID by an obvious change in movement direction or gait. I excluded questionable data from subsequent analyses.

Subjects were not marked; we avoided resampling individuals by focusing on birds in different geographic locations and not resampling the same location repeatedly. We studied birds in both pristine environments with little to no human activity and in areas with frequent human activity. I excluded from analyses observations of individuals in highly visited city parks and individuals that approached humans (e.g., for handouts) rather than fleeing.

I classified a species' relative preference for habitat openness by the amount of vegetation as described in Pizzey and Knight (1997). The primary habitat for each species was classified in order of decreasing vegetation density as: dense forest, open forest or rainforest edge, scrubland, wetland, or beach. For analysis, I defined dense forest as closed habitat, and scored all other habitat types as open.

I conducted analyses using SPSS 10 (SPSS 2000). For all species with >25 observations (68 species), I regressed starting distance against FID fitting both linear and logarithmic models. I performed a subsequent series of $t$-tests and contingency table analyses aimed at understanding factors that might account for the presence of linear or logarithmic regressions. Additionally, I fitted a general linear model to the entire data set to explain variation in FID as a function of starting distance, species, and the interaction between them. Here, the key variable is the interaction, which would identify whether species responded similarly in their relationship between starting distance and FID.

## RESULTS

In 64 of 68 species, I found a significant positive linear relationship between starting distance and FID (Table 1). The explained variation and slope were quite variable. Linear regressions explained more variation than did logarithmic regressions for 32 species, while logarithmic regressions explained more variation than linear for 36 species. I detected no difference in the average range of starting distances ($P = 0.18$), the minimum starting distance ($P = 0.72$), or the maximum starting distance ($P = 0.20$) among species as a function of the shape (log or linear) of the relationship between starting distance and FID. The shape of the relationship was not influenced by the openness of the habitat ($P = 0.57$). Species ($P < 0.001$), starting distance ($P < 0.001$), and the interaction between species and starting distance ($P < 0.001$) were all significant terms in the analysis of covariance model that explained significant variation in FID (adjusted $R^2 = 0.673$, $P < 0.001$). The largest partial $\eta^2$ (a measure of effect size) was seen with the interaction ($\eta^2_{\text{interaction}} = 0.192$, $\eta^2_{\text{species}} = 0.068$; $\eta^2_{\text{starting distance}} = 0.070$). This significant and relatively important interaction indicates that the relationship between starting distance and FID varied by species.

## DISCUSSION

As predicted by the Ydenberg and Dill (1986) model, FID was variable among individuals within a species and yet was shown in my research to be influenced by the starting distance. Starting distances varied widely (Table 1), but only about half of the species had logarithmic relationships between starting distance and FID. I found no obvious differences in starting distances for those species with linear or logarithmic relationships. A measure of habitat openness also did not explain significant variation. My results suggest that for those species without logarithmic relationships, $D_{max}$ may be very large and not easy to estimate. Moreover, because I found significant regressions in virtually all observed species, I infer the effect of starting distance to be a general phenomenon that applies to many species. I am aware of no other single factor that systematically influences FID across a wide range of species.

Starting distance will generally influence FID in zone II (Fig. 1)—the zone of trade-offs. Animals detecting an approaching predator from afar may flee to reduce the cost of their escape. For instance, by fleeing early, an animal need not escape at maximum velocity. Alternatively, the benefit of remaining declines as a predator continues its approach. For instance, if animals must allocate attention (Dukas and Kamil 2000) to monitoring an approaching predator, the value of remaining in a particular patch should decline in response to the predator's consistent approach. My results are consistent with this attentional interpretation.

## MANAGEMENT IMPLICATIONS

Taken together, my results suggest that birds optimize their escape behavior by monitoring potential threats and retreating from them while the cost of escape is still low. Thus, and in contrast to previous suggestions (Holmes et al. 1993, Lord et al. 2001), I suggest that to properly quantify a species' FID, the starting distance should not be standardized because the dynamic nature of escape is not then incorporated into buffer-zone design. Because we expect escape to be optimized and because FID explains considerable variation in escape distance, other strategies are required.

One option is to begin walking toward individuals at a variety of distances and aim to collect a relatively even distribution of starting distances. By collecting FID data across a wide range of starting distances, managers will be able to determine whether an obvious asymptotic relationship (and therefore any evidence of $D_{max}$) becomes apparent. If an obvious $D_{max}$ does not emerge from such a sampling protocol, a wide range of starting distances will allow managers to obtain a representative estimate of both the mean and variance of FID. Highly variable FIDs (Table 1) suggest that conservative set-back distances should be much larger than the mean FID.

In some cases, managers may be able to estimate the distance beyond which animals trade off risk. If so, $D_{max}$ may be a useful measure with which to define set-back distances.

Behavioral ecologists interested in studying decision making in the zone of trade-offs should use starting distance as a covariate, as should those who use FID to study how birds perceive human disturbance (e.g., Cooke 1980, Holmes et al. 1993). Natural history characteristics likely will influence a species' FID. Species living in closed habitats are likely to have smaller and less variable FIDs because of a diminished opportunity to first respond at large distances. Interestingly, even for species in closed habitats, a relationship exists between starting distance and FID. In contrast, species living in the open should have greater opportunities for trade-offs, and therefore will have larger and more variable FIDs.

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