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Escape Behaviour of Breeding Birds in Riparian Habitats of North Africa: Effect of Climate and Elevation Patterns

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Abstract: Understanding how birds respond to human disturbance is essential for predicting behavioural adaptation under environmental change. We assessed fearfulness in riparian bird species during the breeding season in a montane region of north-eastern Algeria using flight initiation distance (FID) as a behavioural proxy. We analysed 479 FID observations from 39 species recorded in the Aurès Highlands and tested the effects of environmental predictors using two phylogenetic generalised least squares (PGLS) models: one including precipitation and the other - including spring temperature, alongside elevation and additional covariates. Mean FID was 22.39 ± 8.75 m (range: 5–53 m), with most values between 10 and 30 m. Species identity strongly influenced FID, explaining 38% of the variance, whereas site effects were weak. Both PGLS models received similar support (ΔAICc = 0.35), indicating that precipitation- and temperature-based climatic formulations explained the data equally well. Starting distance was the strongest predictor of FID, with a very large positive effect (r = 0.96, 95% CI: 0.93–0.98). Elevation had a consistent large positive effect in both models (r = 0.49 and 0.47, correspondingly), showing that birds at higher altitudes initiated escape at greater distances. Climatic conditions also shaped FID: higher precipitation was associated with shorter FID (β = -0.02, p = 0.005), whereas higher spring temperatures were associated with longer FID (β = 0.02, p = 0.006). Together, our results suggest that birds inhabiting warmer and drier environments are generally more fearful than those in cooler or wetter areas. Raptor abundance showed only weak associations with FID, body size had no clear independent effect, while vegetation cover was not retained in the final models, possibly owing to sampling limitations or because its influence was overridden by climatic factors and unmeasured habitat conditions. Phylogenetic analyses detected no signal in FID (Pagel's λ = 0), indicating that closely related species did not exhibit more similar escape responses than expected by chance.

Key words: Altitude, FID, phylogenetic signal, precipitation, spring temperature

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Introduction

Riparian habitats in the Mediterranean ecoregion function as ecotones between aquatic and terrestrial habitats, playing a crucial role in the life cycles of many organisms and being essential for supporting biodiversity (Naiman et al. 1993, Capon et al. 2013). These distinct ecosystems host both specialist species that depend on wet environments and generalist species that can exist elsewhere (Ramey & Richardson 2017). Particularly, in more arid regions, such as North Africa, riparian zones serve as critical refuges for many organisms, attracting, for example, numerous bird species due to favourable conditions, such as high biological productivity (affecting food availability) and cooler and wetter microclimate (Fleishman et al. 2002, Palmer & Bennett 2006).

The avifauna of riparian habitats is increasingly threatened by the degradation of these habitats, mostly driven by human-related activities that are often established nearby to accessible water resources. These pressures, further impacted by climate change, result in significant ecological degradation, requiring management strategies that holistically protect all organisms dependent on these ecosystems. For this purpose, behavioural responses of organisms to human disturbance have long been important for land conservation and management (Morelli et al. 2022). Wildlife managers often use such behavioural measures to identify thresholds beyond which animals experience minimal disturbance from humans. One widely applied measure is flight initiation distance (FID), the distance at which a bird, when approached by a human intruder, initiates escape (Blumstein et al. 2005, Cooper & Blumstein 2015). This escaping behaviour can be used to measure tolerance to human disturbance and illustrate human impacts on birds (Blumstein 2003, 2006a, Bötsch et al. 2018). Importantly, FID is considered a reliable metric for quantifying risk-taking tendencies in birds and serves as an effective tool for establishing protective buffer zones, where human activity is minimised to reduce disturbance around critical habitats (Livezey et al. 2016, Morelli et al. 2022). This component of bird behaviour has been extensively studied worldwide, particularly in Europe and North America. These studies have given rise to several key hypotheses, such as that FID is a personality trait (Blumstein et al. 2003), resident birds are more behaviourally plastic than migrants (Morelli et al. 2022), diet could affect the sensitivity of birds to humans (Nepali et al. 2024) and that urban birds are more tolerant to humans than rural ones (Bonier et al. 2007, Díaz et al. 2013, Mikula et al. 2023). All these assumptions and others remain under active research and comparative analyses consider also key life-history and eco-environmental factors, such as season, climate, latitude and altitude (Capon et al. 2013, Díaz et al. 2021, Ekanayake et al. 2022).

However, studies of this nature remain highly limited across African countries and FID research is virtually absent in North Africa, with the exception of a single study by Halassi et al. (2022). This lack of research is striking given the region's high biodiversity, increasing anthropogenic pressures and vulnerability to climate change. Without empirical data on how local species respond to human disturbance, conservation planning in North Africa risks overlooking behavioural thresholds that are critical for species persistence in human-disturbed areas. Addressing this gap is, therefore, essential for developing context-specific management strategies and establishing effective protective buffer zones in this region. In this study, we aim to assess the degree of fearfulness in riparian bird species during their breeding season in a montane region (the Aurès Highlands) of north-eastern Algeria. We used flight initiation distance (FID) as a behavioural proxy to quantify fear responses of birds to humans, while accounting for key environmental characteristics of the region. Specifically, we aimed to test the applicability of the previously proposed hypotheses on drivers of FID in a distinct geographical context. Due to the montane character of the region and its position as a barrier between the Algerian desert (semi-arid to arid climate) and the Tell Region (semi-arid to humid climate), the study area constitutes an excellent natural laboratory to test the effects of two important abiotic factors (climate and altitude) on this important animal behaviour. Several mechanisms by which FID may be affected by climatic variation were previously suggested by Diaz et al. (2021), who concluded that birds adjust their FID to variation in temperature and precipitation according to the harshness and riskiness of their habitat conditions, their body size and their position within the trophic food web. Regarding altitudinal variation, Andrade and Blumstein (2020), who examined antipredator behaviour along elevational and latitudinal gradients in dark-eyed juncos *Junco hyemalis*, reported that elevation can produce effects opposite to those of latitude, primarily because predation risk changes along elevational gradients. These climate- and altitude-driven predictions led us to hypothesise that FIDs would be longer under higher temperatures due to reduced energetic needs and at higher

elevation due to a change in predation pressure. In contrast, FIDs were expected to decrease in more humid conditions (higher precipitation), due to decreased efficiency of foraging (Díaz et al. 2021).

Materials and Methods

Study region

We collected data at 62 riparian sites located in a mountainous region of north-eastern Algeria (Fig. 1). The Aurès Highlands (34°90′ - 35°60′ N and 5°10′ - 7°10′ E) cover an area of 12,428 km². The mountains are the largest forested physical boundary between northern and southern Algeria and are the first barrier against the vast Sahara Desert, thus serving as a natural divide between the arid climate of the south and the semi-arid to subhumid Mediterranean climate of the north. The study region represents the most significant and the first forested area encountered by migrant birds after traversing the Sahara Desert during spring migration.

FID data

Data were collected daily from sunrise to five hours afterwards during the breeding season (April - June 2023), following a standardised protocol (Stankowich & Blumstein 2005, Blumstein 2006b, Møller 2010, Halassi et al. 2022). Upon locating an individual bird, the observer approached it at a steady walking speed (~3 km/h), while maintaining visual contact and counting the number of steps taken, each step approximating one meter. This allowed estimation of the starting distance (SD), defined as the observer's initial position to the bird at the moment the observer first detected the bird and began the approach, and of the FID, defined as the distance at which the bird took flight in response to the approaching observer. To account for potential effects on FID, several environmental variables were recorded at each observation site (Andrade & Blumstein 2020). To extract the value of each variable, the methodology used was based on satellite data analysis (the processing of all variables was per-

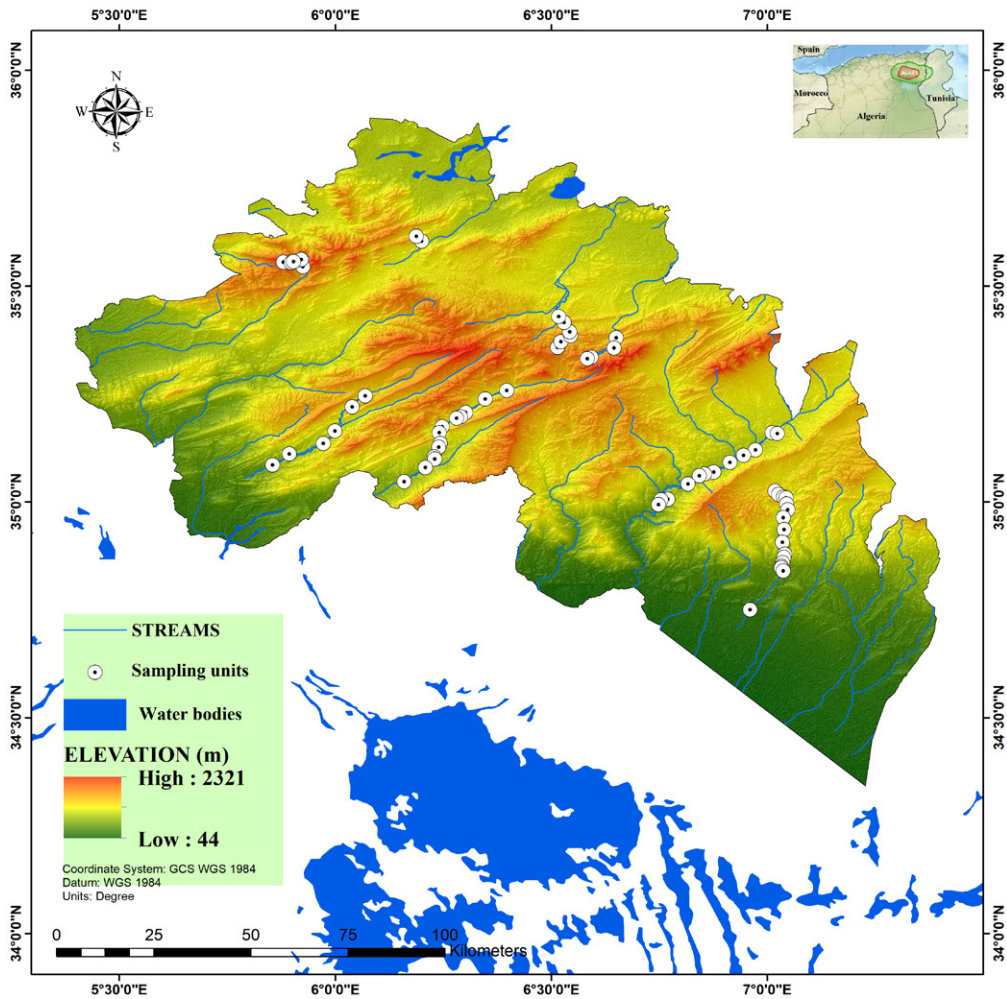

Fig. 1. Altitudinal variation and points of observation across the Aurès Highlands, north-eastern Algeria.

formed in ArcGIS), as well as on measurements and observations in the field (Table 1). As a proxy of predation risk, the number of raptors observed at each site was also recorded prior to initiating the evaluations of FID. These observations were conducted systematically at each site to ensure consistency across sampling locations. Each of the 62 sampling riparian units had a radius of approximately 180 m and included parts of the river bed, the floodplain and the adjacent upland (Fig. 1). The choice of a 10-hectare (180 m radius) area was based on both ecological and methodological considerations. Specifically, that area was sufficient to capture the full width of the riparian corridor influenced by stream hydrology, microclimatic gradients and edge effects associated with adjacent land uses (Decocq 2002, Goebel et al. 2003). To minimise disturbance and avoid pseudoreplication, we did not resample the same bird individual during a given visit and we waited at for at least 2 min before targeting another bird at the same site (Blumstein et al. 2003).

Information on bird species traits (body size and feeding guild) was obtained from two online databases - AviBase (2025) and Avian Diet Database (2023), using species-level data compiled by Hurlbert et al. (2021) and Clements (2023).

Statistics

We log-10-transformed FIDs and SDs, while all continuous variables were z-standardised (to have a mean of 0 and a standard deviation of 1) before analysis in order to reduce skewness in the distributions and approximate normality. We tested whether flight initiation distance (FID) varied among species across stations using a two-way ANOVA with species, site and their interaction as factors. Effect sizes (partial η^2) were calculated to quantify the proportion of variance explained by each factor. Because annual precipitation was found to be correlated with annual temperature, we addressed multicollinearity by analysing these variables in separate models. Latitude was also highly correlated with altitude and showed limited variation across sampling sites; therefore, to avoid redundancy and improve model interpretability, it was excluded from the analyses.

Closely related species are generally more likely to exhibit similar traits than distantly related species, which can violate the assumption of independence among observations due to shared evolutionary history (Freckleton et al. 2002). To account for phylogenetic non-independence among sampled species, we fitted phylogenetic generalised least squares (PGLS) regression models weighted by sample size, implemented in the R statistical environment using packages *ape*, *nlme* and *geiger* (see: Garamszegi & Møller 2007, Soler & Avilés 2010, Díaz et al. 2013). In these models, phylogenetic covariance among species was incorporated using a correlation structure based on Pagel's lambda (λ), estimated directly from the data by maximum likelihood. Lambda quantifies the strength of the phylogenetic signal in the residual variation of the response variable, ranging from 0 (phylogenetic independence) to 1 (trait covariance consistent with a Brownian motion model of evolution; Freckleton et al. 2002). Model parameters were estimated using maximum likelihood. To account for heteroscedasticity associated with differences in sampling effort, models were weighted by the inverse of replicate number as a proxy of variance to be used in the variation function structure (argument "weights" of the "gls" function: Paradis et al. 2004; Garamszegi & Møller 2010).

We fitted two sets of PGLS to explain variation in FID:

- Temperature models: FID ~ SD + Tspring + all predictors

- Precipitation models: FID ~ SD+ Pyear + all predictors

We acknowledge that direct temperature measurements would have been preferable; however, as these were not available, we used spring temperature as the most relevant proxy, since it coincides with the breeding period of the observed birds. We used annual precipitation as a proxy for ecosystem productivity and food availability, as rainfall strongly influences primary production and resource abundance in Mediterranean ecosystems. Previous studies have shown that SD is strongly positively correlated with FID (Blumstein 2006a), thus it was included as a covariate.

An information-theoretic approach based on Akaike's Information Criterion corrected for small sample size (AICc) was used to compare the competing models (temperature versus precipitation) and evaluate their relative support. To account for phylogenetic uncertainty, all analyses were repeated across 100 phylogenetic trees obtained from BirdTree.org (Jetz et al. 2012), based on the Ericson backbone avian phylogeny. From these 100 trees, we used the *consensus* function in the *ape* package in R to calculate a 50% majority-rule consensus phylogeny (Paradis et al. 2004) (Supplementary file 1).

Finally, effect sizes were reported as mean regression coefficients with 95% confidence intervals across all trees. We evaluated the magnitude of associations between FID and predictor variables based on effect sizes and their 95% CI, as com-

Table 1. Summary of environmental variables.

Variable	Description and source	Mean ± SD (Min-Max)
Total vegetation cover	Surface per 10-hectare plot Observation in the field and Satellite data (Copernicus Data Space Ecosystem, Google Earth Engine, NASA POWER Data Access Viewer, ESA WorldCover and Esri (2020).	44.12±22.85% (2-90%)
Distance to human habitation	As a proxy of urbanization level. The distance between the sampling plot center and the nearest human habitation.	167.68±316.97m (0-1400m)
Altitude	Elevation (m a.s.l.)	1020.96± 325.23m (420-1795m)
Raptors	Number of individuals observed (direct count)	0.97±1.33 (0-7 individuals)
Spring temperature	Extracted from publicly available gridded datasets (resolution: 0.5º × 0.5º) available via the NASA POWER Data Access Viewer Calculated as the mean temperature during the breeding season months: March, April and May.	15.2±2°C (12.87-20.83°C)
Annual precipitation	As a proxy for ecosystem productivity and food. Calculated as the total accumulated rainfall for the year 2023.	303.24±56.61mm (208.16-382.58mm)

puted from P values of t-tests according to Cohen (1988). Following Diaz et al. (2013), Cohen effect sizes were interpreted as small ($r \approx 0.10$), medium ($r \approx 0.30$) and large ($r \geq 0.50$), corresponding approximately to 1%, 9% and 25% of the variance explained, respectively.

Results

Summary statistics for FID

We obtained information on 479 flight initiation distance (FID) observations from 39 bird species during their breeding period in the Aurès Highlands, north-eastern Algeria (Supplementary file 1). The most frequently observed bird species were house sparrow *Passer domesticus*, woodchat shrike *Lanius senator*, spotted flycatcher *Muscicapa striata*, European serin *Serinus serinus* and common blackbird *Turdus merula*, accounting for 32% of the total observations (Supplementary file 2). Most FID values ranged between 10 and 30 m (Supplementary files 2, 3), with a mean of 22.39 m (SD = 8.75 m; range = 5–53 m). The two-way ANOVA revealed a strong effect of species identity on flight initiation distance ($F_{(38,402)} = 6.65$, $p<0.001$), whereas neither site ($F_{(1,402)} = 2.82$, $p = 0.09$) nor their interaction with species ($F_{(37, 402)} = 1.17$, $p = 0.23$) were significant. Effect size estimates indicated that species identity explained a large proportion of the variance in FID (38%), highlighting strong differences among species in mean FID. In contrast, site and species-by-site effects were weak, indicating little influence of spatial variation or context-dependent differences in FID.

Response to altitude and climate changes

Both phylogenetic generalised least squares models (Table 2) revealed highly consistent predictors of flight initiation distance, with nearly equivalent support based on information criteria (precipitation model: AICc = -168.40; temperature model: AICc = -168.05; ΔAICc = 0.35), indicating that both climatic formulations explained the data similarly well. In both models, starting distance was by far the strongest predictor of FID ($\beta \approx 1.08–1.09$, $p < 0.001$), showing a very large positive effect size ($r = 0.96$, 95% CI: 0.93–0.98). Altitude was also a consistent

and significant predictor, with large positive effects in both models (r = 0.49 and 0.47, correspondingly), suggesting greater escape distances at higher elevations. Regarding climate, the precipitation model showed that higher precipitation was associated with lower FID (β = -0.02, p = 0.005), with a large negative effect (r = -0.46, 95% CI: -0.67 to -0.16). Conversely, the temperature model indicated that higher spring temperatures were associated with greater FID (β = 0.02, p = 0.006), with a large positive effect (r = 0.45, 95% CI: 0.15–0.67). Together, these findings suggested that birds inhabiting warmer and drier environments tended to initiate escape at greater distances than those in cooler or wetter areas. Raptor abundance showed a weaker but generally negative association with FID in both models, reaching significance only in the temperature model (r = -0.33, 95% CI: -0.59 to -0.02), indicating slightly shorter escape distances where raptor abundance was higher. Body size had small-to-moderate negative effect estimates in both models, but confidence intervals included zero, suggesting no clear independent relationship with FID after accounting for other predictors. Overall, the results indicated that FID was primarily determined by detection context (starting distance), secondarily - by elevation and climate and it was only weakly related to predation pressure or body size.

Phylogenetic analyses indicated no detectable phylogenetic signal in FID. Pagel's λ was estimated at or near zero in all models (λ = 0), demonstrating that closely related species did not show more similar escape distances than expected by chance. This conclusion was further supported by the trait-mapped phylogeny, in which high and low FID values were dispersed across multiple unrelated lineages rather than clustered within particular clades (Fig. 2). Together, these findings indicated that variation in FID in our study area was more strongly associated with contemporary ecological conditions than with shared ancestry.

Discussion

Most FIDs in our study ranged between 10 and 30 m, with a mean of 22.39 m. These values are considerably higher than those reported for European cities: approximately five times higher than in Budapest (Hungary) and twice as high as in Toledo (Spain) (Morelli et al. 2022). The study region is character-

Table 2. Results of phylogenetic generalised least squares (PGLS) models examining the effects of altitude and climate on log-transformed flight initiation distance (FID). Shown are parameter estimates (β), standard errors (SE), t-values, p-values and effect sizes expressed as correlation coefficients (r) with 95% confidence intervals shown in brackets.

Feature	Estimate	SE	T-value	P-value	Effect size (r, 95%CI)
Precipitation model	**AICc = -168.4**				
Intercept	-0.14	0.06	-2.39	0.02	
Starting Distance	1.08	0.04	21.91	<0.001	0.96 (0.93, 0.98)
Altitude	0.02	0.008	3.27	0.002	0.49 (0.21, 0.70)
Precipitation	-0.02	0.008	-2.97	0.005	-0.46 (-0.67, -0.16)
Raptor Abundance	-0.008	0.004	-1.93	0.06	-0.31 (-0.57, -0.004)
Body size	-0.01	0.01	-1.66	0.10	-0.27 (-0.54, 0.040)
Temperature model	**AICc = -168.05**				
Intercept	-0.14	0.06	-2.42	0.02	
Altitude	0.02	0.006	3.12	0.003	0.47 (0.19, 0.68)
Starting Distance	1.09	0.04	21.93	<0.001	0.96 (0.93, 0.98)
Spring temperature	0.02	0.006	2.89	0.006	0.45 (0.15, 0.67)
Raptor Abundance	-0.008	0.004	-2.06	0.04	-0.33 (-0.59, -0.02)
Body size	-0.01	0.01	-1.73	0.09	-0.29 (-0.55, 0.02)

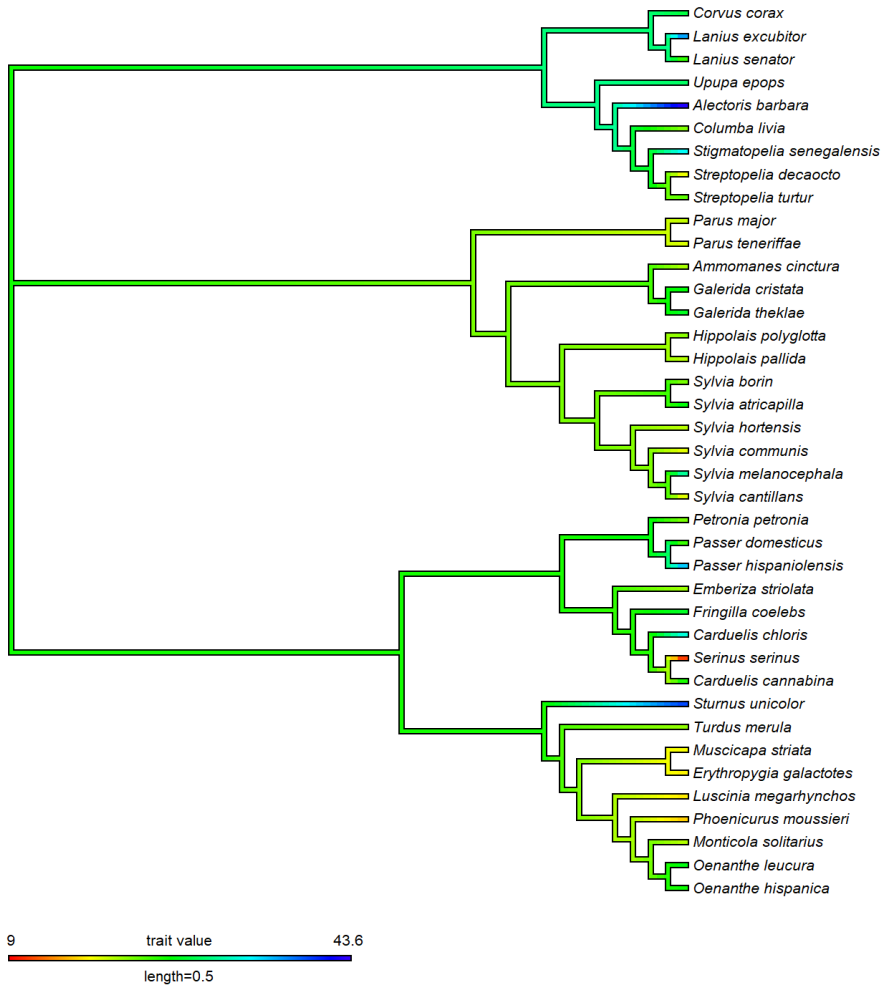

Fig. 2. Consensus phylogeny of the 39 bird species included in the study, with branch colours representing species-specific flight initiation distance (FID) values. Warmer colours indicate lower FID and cooler colours indicate higher FID.

ised as a traditional farming landscape, comprising limited areas of transhumance pastoralism, scattered settlements, oases and remnant forest patches, giving it an overall rural vocation. The characteristics of the region support the conclusion that urban birds are more tolerant to humans than rural ones (Bonier et al. 2007, Díaz et al. 2013, Mikula et al. 2023). Additionally, our findings are consistent with the latitude association hypothesis that expects FIDs to decrease with increasing latitude (Díaz et al. 2013). In other words, birds become more sensitive to human approach at lower latitudes, initiating flight earlier than their higher-latitude counterparts.

Our results showed that species identity explained a large proportion of the variance in FID (38 %), indicating that escape behaviour was strongly determined by species-level traits. In contrast, the effects of site and species-by-site interactions were comparatively small, suggesting that local environmental factors played a minor role. Together, these findings highlight that FID is driven by intrinsic species characteristics, supporting the hypothesis that flight initiation distance (FID) can be considered a species-specific trait (Blumstein et al. 2003).

We find that birds' risk assessment was also influenced by climatic and altitude variation; however, the effect sizes of these altitude-climate-behaviour relationships were small compared to the strong influence of starting distance. This finding reinforces previous recommendations to include starting distance as a covariate in models of FID (Blumstein 2003), as failing to do so may obscure the true drivers of escape behaviour.

Both phylogenetic generalised least squares models (spring temperature and precipitation models) revealed highly consistent predictors of flight initiation distance (ΔAICc = 0.35), indicating that both climatic formulations explained the data similarly well.

We found that FID decreased with increasing precipitation. Precipitation can strongly influence food availability and other ecological conditions

relevant to reproductive success (Arct et al. 2025). However, the observed pattern in our study is more consistent with the hypothesis that more humid climatic conditions are associated with reduced foraging success (Díaz et al. 2021). Under such conditions, birds may need to invest more time and effort in foraging, leaving less opportunity to engage in vigilance and, thereby, tolerating closer human approaches. This interpretation is further supported by the fact that our study was conducted during the breeding season, when parental energetic demands are high and trade-offs between vigilance and provisioning are most pronounced. Spring temperature also carries meaningful explanatory power. The positive association between temperature and FID could be due to reduced caloric needs or a reduction in food availability (Díaz et al. 2021).

Both of our models retained elevation as a significant predictor, with FID increasing at higher altitudes (Table 2). This finding is consistent with Andrade & Blumstein (2020), who examined antipredator behaviour along elevational and latitudinal gradients in dark-eyed juncos. Andrade & Blumstein (2020) reported that elevation can have effects opposite to those of latitude, primarily because predation risk changes along elevational gradients. Our results support their conclusion and highlight the need for further research to clarify how predation pressure and other relevant traits vary with elevation and how these shape escape behaviour across species. Interestingly, our direct measure of predation risk, based on the number of raptors observed, had a weak effect on FIDs. This might be due to raptor counts being a poor proxy for overall predation risk, as many other predators (e.g. mammals, corvids, snakes) may significantly contribute to perceived danger. An alternative explanation could be that other factors, such as habitat structure or visibility, might be more important drivers.

Vegetation cover, a factor widely documented as influencing FID (Finney et al. 2005, Stankowich & Blumstein 2005), was also not retained in our final models (Supplementary file 4). This is not unprecedented, as Osorio-Beristain et al. (2018) also reported a non-significant effect of vegetation cover on escape behaviour. One possible explanation for this result is the spatial scale at which vegetation cover was quantified. Our estimates were based on 10 ha plots, which may represent too coarse a scale to capture the microhabitat conditions most relevant to birds' risk perception. Confirming, thereby, that such studies should consider measuring vegetation structure at a finer resolution, closer to the birds' immediate environment, to better assess its role in shaping escape decisions.

Across species, FID is typically positively correlated with body size (Fernández-Juricic et al. 2006; Virkkala & Lehikoinen 2014). Interestingly, body size was not a significant predictor in either of our models. The way birds adjust their FID to variation in temperature and precipitation is expected to depend on habitat harshness, predation risk, body size and trophic position (Díaz et al. 2021). Our study system, the Aurès Highlands , located at the northern edge of the Algerian Sahara, represents the southernmost breeding limit for many Palearctic bird species (all the studied species) (Benchaiba et al. 2026). Populations near the edge of their ecological or geographic range are often exposed to more stressful conditions and reduced habitat suitability (Orme et al. 2019, Tellería et al. 2021). Under such conditions, climate effects may become more pronounced and could override or buffer the influence of other environmental and intraspecific variables, including body size.

While the importance of this research lies in reporting one of the few studies documenting the effects of altitude on bird fearfulness, particularly within a North African context, a main caveat of our results should be acknowledged. The effect sizes estimated for each predictor in both models varied in both magnitude and precision, with one strong and precisely estimated relationship (starting distance r= 0.96, CI 95% = 0.93-0.98) and several moderate effects showing wider confidence intervals, indicating substantial uncertainty (Table 2). Such variation is expected in FID studies, given the multifactorial nature of escape behaviour and ecological heterogeneity across contexts. Future work should increase sample sizes across environmental gradients and improve balanced sampling across species and habitats to enhance precision. In addition, explicitly modelling interactions among climatic, topographic and biotic factors, as well as integrating fine-scale predator and vegetation data, would help clarify the relative importance of direct versus indirect drivers of variation in FID.

Conclusion

Our study demonstrates that flight initiation distance in birds is shaped by a combination of climatic and topographic factors after accounting for starting distance and phylogenetic effects. FID decreased with increasing precipitation, suggesting a potential trade-off between vigilance and foraging under wetter conditions, particularly during the energetically demanding breeding season. In contrast, higher temperatures were associated with earlier escape responses, indicating that warming conditions may

increase perceived risk or physiological stress. Elevation also influenced FID, but the weak association with raptor abundance indicates that the elevational pattern is unlikely to be driven primarily by variation in predation pressure alone. Finally, several well-known predictors of FID, including vegetation cover, body size and raptor abundance, were not retained as significant in our models, possibly owing to sampling limitations or because their influence was overridden by climatic factors and unmeasured habitat conditions. Together, these results underscore the importance of considering local climatic context when applying general models of antipredator behaviour and call for more detailed research on how climate and predation pressures interact to shape risk perception across species and regions.

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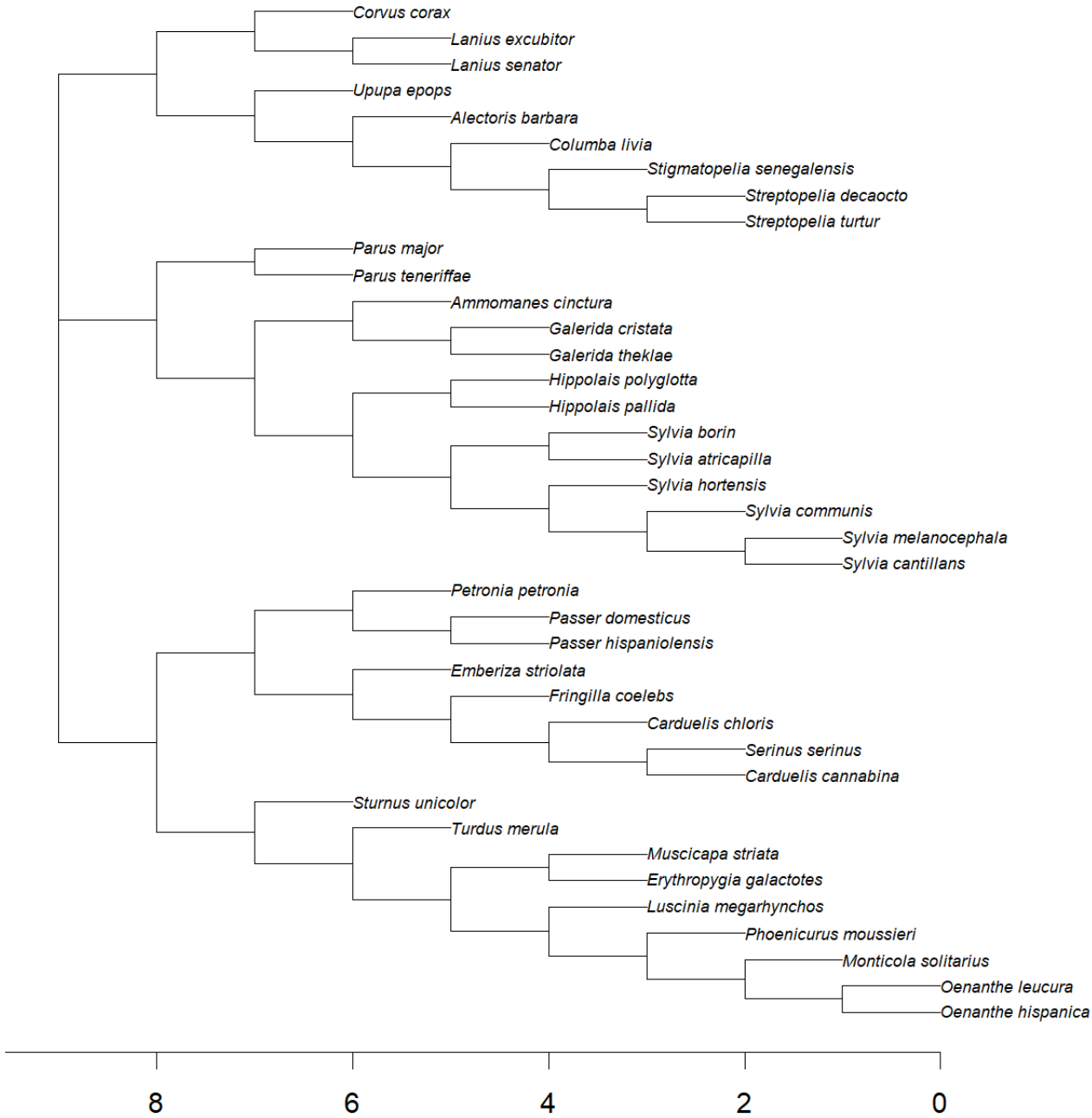
Supplementary file 1. 50% Majority-Rule Consensus Phylogeny.

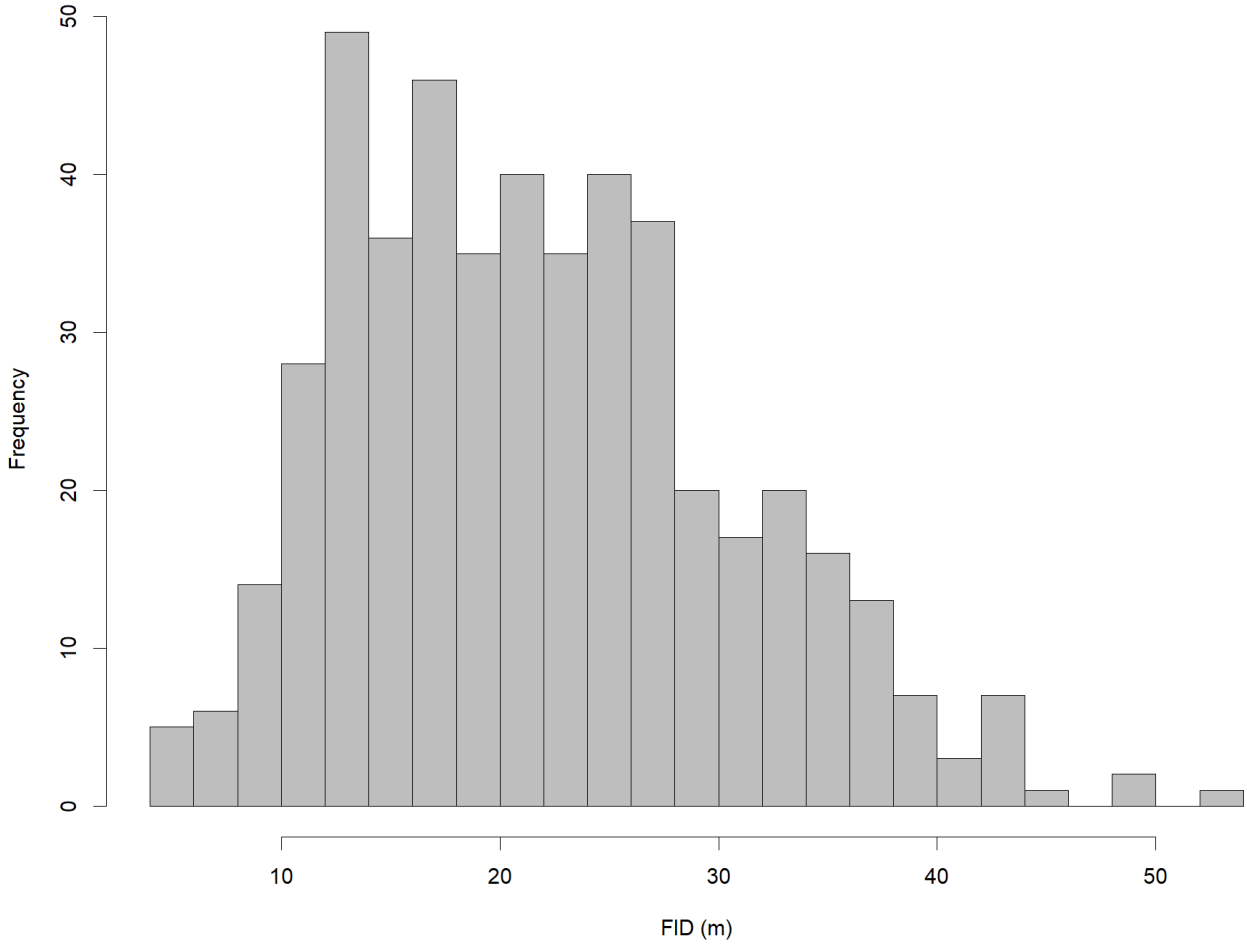


Supplementary file 2. Summary statistics of FIDs estimates for all species.

Table I. Summary statistics of FIDs estimate for all species.

Species	Status	Food	n	Mean	STD	Min	Max	Fr %
Alectoris barbara	SED	Herbivore	4	34.25	12.50	22	46	0.84
Ammomanes cinctura	SED	Herbivore	3	22.67	8.50	14	31	0.63
Cercotrichas galactotes	MB	Invertivore	13	16.92	5.44	6	27	2.72
Chloris chloris	SED	Herbivore	6	21.00	8.07	11	32	1.26
Columba livia	SED	Herbivore	26	22.58	8.11	10	37	5.44
Corvus corax	SED	Carnivore	5	38.20	8.04	28	49	1.05
Curruca communis	MB	Invertivore	7	27.43	3.21	23	31	1.46
Curruca hortensis	MB	Invertivore	7	26.86	5.67	17	34	1.46
Curruca iberiae	MB	Invertivore	4	25.75	8.77	16	35	0.84
Cyanistes teneriffae	SED	Invertivore	10	19.80	7.71	8	32	2.09
Emberiza sahari	SED	Herbivore	22	19.50	6.75	9	30	4.60
Fringilla coelebs	SED	Invertivore	14	21.21	6.19	11	31	2.93
Galerida cristata	SED	Herbivore	2	17.00	4.24	14	20	0.42
Galerida theklae	SED	Invertivore	2	32.00	5.66	28	36	0.42
Hippolais polyglotta	MB	Invertivore	20	17.85	5.45	10	33	4.18
Iduna pallida	MB	Invertivore	16	19.44	4.60	14	31	3.35
Lanius excubitor	SED	Carnivore	8	26.25	5.99	15	33	1.67
Lanius senator	MB	Invertivore	29	21.24	6.72	9	34	6.07
Linaria cannabina	SED	Herbivore	5	18.40	2.97	15	23	1.05
Luscinia megarhynchos	MB	Invertivore	15	19.20	6.36	10	32	3.14
Monticola solitarius	SED	Omnivore	5	40.00	8.72	29	53	1.05
Muscicapa striata	MB	Invertivore	31	20.74	6.06	10	35	6.49
Oenanthe hispanica	MB	Invertivore	6	25.33	8.52	13	34	1.26
Oenanthe leucura	SED	Invertivore	20	26.40	7.65	16	43	4.18
Parus major	SED	Invertivore	7	19.57	7.61	11	32	1.46
Passer domesticus	SED	Herbivore	34	15.41	6.79	5	37	7.11
Passer hispaniolensis	SED	Invertivore	4	16.50	9.88	6	28	0.84
Petronia petronia	SED	Omnivore	17	16.88	6.77	6	34	3.56
Phoenicurus moussieri	SED	Invertivore	17	17.53	7.05	5	33	3.56
Serinus serinus	SED	Herbivore	29	21.31	7.87	8	35	6.07
Spilopelia senegalensis	SED	Herbivore	5	37.00	1.87	35	40	1.05
Streptopelia decaocto	SED	Herbivore	16	22.56	5.67	12	32	3.35
Streptopelia turtur	MB	Herbivore	11	33.36	8.43	16	44	2.30
Sturnus unicolor	SED	Omnivore	11	25.82	7.04	12	38	2.30
Sylvia atricapilla	SED	Omnivore	2	9.00	0.00	9	9	0.42
Sylvia borin	MB	Invertivore	7	26.86	5.70	21	36	1.46
Sylvia melanocephala	SED	Omnivore	3	20.33	6.66	16	28	0.63
Turdus merula	SED	Herbivore	30	28.67	8.71	11	43	6.28
Upupa epops	MB	Invertivore	5	43.60	3.78	40	50	1.05

Supplementary file 3. Frequency distribution of flight initiation distance of 39 bird species during their breeding period in the Aurès Highlands, north-eastern Algeria.



Supplementary file 4. Candidate phylogenetic generalised least squares (PGLS) models ranked by AICc for explaining variation in flight initiation distance (FID).

Model ID	(Intercept)	lgSD	lgweight	ZAlt	ZP	ZRap	Zveg	df	logLik	AICc	delta	weight
32	-0,14418	1,087883	-0,01699	0,026971	-0,02397	-0,00811	NA	7	93,05634	-168,5	0	0,261246
30	-0,09098	1,031683	NA	0,031323	-0,02713	-0,00978	NA	6	91,48002	-168,335	0,164734	0,24059
16	-0,17418	1,112761	-0,0217	0,025077	-0,02169	NA	NA	6	90,96586	-167,307	1,193044	0,143874
62	-0,08765	1,029346	NA	0,033139	-0,02562	-0,01009	-0,00468	7	91,79374	-165,975	2,525192	0,073911
64	-0,14121	1,085047	-0,01631	0,027599	-0,02372	-0,00825	-0,00117	8	93,07471	-165,349	3,150342	0,054071
14	-0,11048	1,043559	NA	0,030445	-0,02534	NA	NA	5	88,5661	-165,314	3,185744	0,053122
48	-0,17684	1,115379	-0,02236	0,024428	-0,02201	NA	0,001276	7	90,98635	-164,36	4,139967	0,032966
4	-0,21881	1,152881	-0,03057	NA	NA	NA	NA	4	86,49199	-163,808	4,692257	0,025011
20	-0,19839	1,135966	-0,02732	NA	NA	-0,00633	NA	5	87,49783	-163,177	5,322287	0,018253
8	-0,21149	1,144137	-0,02735	0,006353	NA	NA	NA	5	87,37654	-162,935	5,564877	0,016168
46	-0,10865	1,042234	NA	0,031651	-0,02428	NA	-0,00316	6	88,68976	-162,755	5,745243	0,014774
24	-0,19131	1,12744	-0,02416	0,006295	NA	-0,00627	NA	6	88,41277	-162,201	6,299225	0,011199
36	-0,22463	1,157795	-0,03129	NA	NA	NA	0,00347	5	86,75498	-161,692	6,807999	0,008684
12	-0,21794	1,152573	-0,03078	NA	-0,00119	NA	NA	5	86,52408	-161,23	7,269787	0,006893
52	-0,20374	1,140459	-0,02803	NA	NA	-0,00596	0,002488	6	87,63626	-160,648	7,852255	0,005152
28	-0,19663	1,13511	-0,02756	NA	-0,00178	-0,00647	NA	6	87,57255	-160,52	7,979664	0,004834
40	-0,20582	1,138696	-0,02605	0,007988	NA	NA	-0,00225	6	87,43195	-160,239	8,26086	0,0042
44	-0,22753	1,162543	-0,03341	NA	-0,00653	NA	0,008016	6	87,28747	-159,95	8,549818	0,003635
22	-0,12058	1,050683	NA	0,008735	NA	-0,00843	NA	5	85,8224	-159,827	8,673144	0,003417
56	-0,17788	1,11482	-0,02122	0,009573	NA	-0,00691	-0,00453	7	88,63888	-159,665	8,834904	0,003152
18	-0,11739	1,048439	NA	NA	NA	-0,00892	NA	4	84,22563	-159,275	9,224976	0,002593

Supplementary file 4. Continuation.

Model ID	(Intercept)	lgSD	lgweight	ZAlt	ZP	ZRap	Zveg	df	logLik	AICc	delta	weight
54	-0,11037	1,043726	NA	0,015036	NA	-0,00922	-0,00957	6	86,88979	-159,155	9,345186	0,002442
6	-0,13584	1,059919	NA	0,009271	NA	NA	NA	4	84,13497	-159,093	9,40629	0,002369
60	-0,20695	1,145392	-0,03014	NA	-0,00632	-0,00585	0,006905	7	88,15732	-158,702	9,798034	0,001947
2	-0,13338	1,058098	NA	NA	NA	NA	NA	3	82,48191	-158,278	10,22166	0,001576
38	-0,12855	1,054861	NA	0,01454	NA	NA	-0,00794	5	84,81189	-157,806	10,69417	0,001244
26	-0,11595	1,047499	NA	NA	-0,00103	-0,00902	NA	5	84,24685	-156,676	11,82424	0,000707
50	-0,11845	1,049167	NA	NA	NA	-0,00882	0,000812	5	84,23829	-156,658	11,84138	0,000701
34	-0,13562	1,059669	NA	NA	NA	NA	0,002046	4	82,55673	-155,937	12,56278	0,000489
10	-0,13332	1,058061	NA	NA	-4,58E-05	NA	NA	4	82,48195	-155,787	12,71233	0,000454
58	-0,11704	1,048318	NA	NA	-0,00278	-0,00887	0,002697	6	84,32519	-154,025	14,4744	0,000188
42	-0,13443	1,058952	NA	NA	-0,0025	NA	0,003748	5	82,6213	-153,424	15,07535	0,000139
63	1,134872	NA	0,145349	0,097762	-0,05712	-0,03501	-0,04359	7	41,45906	-65,3052	103,1946	1,02E-23
31	1,150176	NA	0,134679	0,079431	-0,07113	-0,03195	NA	6	39,54733	-64,4697	104,0301	6,72E-24
55	1,130736	NA	0,144153	0,057427	NA	-0,03348	-0,05492	6	39,43769	-64,2504	104,2494	6,02E-24
15	1,14848	NA	0,12941	0,076497	-0,06605	NA	NA	5	37,31768	-62,8172	105,6826	2,94E-24
19	1,159564	NA	0,123105	NA	NA	-0,02956	NA	4	35,95957	-62,7427	105,7571	2,83E-24
47	1,135095	NA	0,138208	0,092118	-0,0535	NA	-0,03772	6	38,58928	-62,5536	105,9462	2,58E-24
39	1,131201	NA	0,137377	0,054464	NA	NA	-0,04861	5	37,03555	-62,2529	106,2469	2,22E-24
3	1,158619	NA	0,118133	NA	NA	NA	NA	3	34,33332	-61,9809	106,5188	1,94E-24
23	1,149968	NA	0,129397	0,019439	NA	-0,02886	NA	5	36,58574	-61,3533	107,1465	1,41E-24
51	1,159431	NA	0,123787	NA	NA	-0,03122	-0,01523	5	36,34185	-60,8655	107,6342	1,11E-24
7	1,14844	NA	0,124948	0,020669	NA	NA	NA	4	34,98603	-60,7956	107,7042	1,07E-24

Supplementary file 4. Continuation.

Model ID	(Intercept)	lgSD	lgweight	ZAlt	ZP	ZRap	Zveg	df	logLik	AICc	delta	weight
27	1,162218	NA	0,121847	NA	-0,00633	-0,03002	NA	5	36,02722	-60,2363	108,2635	8,09E-25
35	1,158482	NA	0,118431	NA	NA	NA	-0,01124	4	34,52663	-59,8768	108,623	6,76E-25
11	1,160202	NA	0,117332	NA	-0,0038	NA	NA	4	34,35584	-59,5352	108,9646	5,70E-25
59	1,156465	NA	0,125388	NA	0,006973	-0,03123	-0,02002	6	36,38737	-58,1497	110,35	2,85E-25
43	1,155547	NA	0,120013	NA	0,006899	NA	-0,01598	5	34,56722	-57,3163	111,1835	1,88E-25
1	1,337756	NA	NA	NA	NA	NA	NA	2	27,88885	-51,4444	117,0554	9,97E-27
17	1,344435	NA	NA	NA	NA	-0,02327	NA	3	28,60253	-50,5193	117,9804	6,28E-27
9	1,338951	NA	NA	NA	-0,01235	NA	NA	3	28,06335	-49,441	119,0588	3,66E-27
33	1,338039	NA	NA	NA	NA	NA	-0,01011	3	28,0011	-49,3165	119,1833	3,44E-27
5	1,337803	NA	NA	0,006237	NA	NA	NA	3	27,93256	-49,1794	119,3204	3,21E-27
13	1,343638	NA	NA	0,053678	-0,05665	NA	NA	4	29,09824	-49,02	119,4798	2,97E-27
25	1,346209	NA	NA	NA	-0,01468	-0,0245	NA	4	28,85691	-48,5373	119,9624	2,33E-27
49	1,345209	NA	NA	NA	NA	-0,02468	-0,01323	4	28,79947	-48,4225	120,0773	2,20E-27
29	1,351312	NA	NA	0,055274	-0,06039	-0,02544	NA	5	30,00181	-48,1854	120,3143	1,95E-27
21	1,344398	NA	NA	0,004846	NA	-0,02301	NA	4	28,6298	-48,0831	120,4166	1,86E-27
37	1,33867	NA	NA	0,023778	NA	NA	-0,02635	4	28,35239	-47,5283	120,9715	1,41E-27
41	1,338843	NA	NA	NA	-0,01036	NA	-0,00302	4	28,06891	-46,9613	121,5384	1,06E-27
45	1,343588	NA	NA	0,059578	-0,05112	NA	-0,01582	5	29,24626	-46,6743	121,8254	9,18E-28
53	1,346019	NA	NA	0,024868	NA	-0,02519	-0,03027	5	29,19991	-46,5816	121,9181	8,77E-28
57	1,346092	NA	NA	NA	-0,01092	-0,0248	-0,00577	5	28,87789	-45,9376	122,5622	6,35E-28
61	1,351594	NA	NA	0,062585	-0,05377	-0,02657	-0,01941	6	30,23391	-45,8428	122,6569	6,06E-28