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Personality and movement behaviour in Galápagos short-eared owls (Asio flammeus galapagoensis)

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# Zusammenfassung

Persönlichkeit bei Tieren kann messbaren Einfluss auf deren Fitness, Life History und wahrscheinlich sogar deren Evolution. Nicht nur das, konstante interindividuelle Unterschiede im Verhalten von Schlüsselarten wie Greifvögel und Eulen können ganze Tiergemeinschaften beeinflussen. Die Galápagos Sumpfohreule (*Asio flammeus galapagoensis*) ist eine Unterart der Sumpfohreule (*A. flammeus*) die auf den Galápagos Inseln endemisch ist und auf manchen Inseln wie Floreana der einzige heimische große Beutegreifer. Generell ist wenig über die Morphologie, Ökologie und das Verhalten dieser Unterart bekannt. Ich beschreibe in meiner Masterarbeit zuerst die aktuell vollständigste Liste an morphologischen Messungen, sowie beschreibe auch Methoden das Geschlecht der Individuen nur anhand von Feldmethoden zu bestimmen. Außerdem zeige ich, dass diese Unterart einen höheren Grad an Geschlechtsdimorphismus aufzeigt als von den anderen Unterarten bekannt ist. In den nächsten zwei Teilen meiner Arbeit habe ich mich folgenden Fragen zugewandt: 1) Gibt es messbare und konstante Unterschiede zwischen den Individuen im Verhalten dieser Unterart die als Persönlichkeit gelten könnten? und 2) Beeinflussen diese Eigenschaften die Bewegung im Raum der Eulen? Ich habe konstante individuelle Unterschiede entlang der Mut-, Aggressivität- und Aktivität-Achse gefunden. Aber nur entlang der Aktivität-Achse erfüllen die Verhaltensunterschiede die Kriterien von Persönlichkeit, nämlich Beständigkeit in verschiedenen Kontexten und in der Zeit. Es wurde kein Einfluss auf deren Bewegung gefunden, aber Weibchen bewegen sich über größere Flächen als Männchen.

# Abstract

Personality in animals can have notable effects on their fitness, life history and even evolution. Not only that, consistent inter-individual behavioural differences in keystone species such as birds of prey can shape whole animal communities. The Galápagos short-eared owl (*Asio flammeus galapagoensis*) is a subspecies of the short-eared owl (*A. flammeus*) that is endemic to the Galápagos Islands and the only native large predator on certain islands, such as Floreana. In general, little is known about this subspecies' morphology, ecology, and behaviour. Thus, in the first chapter of my thesis I provide the most complete set of morphological measurements to date for this subspecies and describe methods to sex individuals in the field. Additionally, I show that this subspecies has a higher degree of sexual dimorphism than what is known from other subspecies. In the next two chapters, I tackled the questions of: 1) Does this subspecies exhibit individual behavioural differences that are consistent across contexts? and 2) do these traits influence individuals' landscape-level movements? I found that there are consistent individual differences along the aggressiveness, boldness, and activity axes. But only along the activity axis the behavioural differences fulfill the criteria of personality, namely consistency across contexts and time. No link to their movement was found, but female Galápagos short-eared owl moved over larger areas than males.

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# Chapter 1: Morphometrics and sexing of the Galápagos short-eared owl (*Asio flammeus galapagoensis*)

**Abstract**

The Galápagos short-eared owl (*Asio flammeus galapagoensis*) is a subspecies of the short-eared owl (*A. flammeus*) that is endemic to the Galápagos Islands. While some studies have investigated this subspecies' diet and genetics, little has been published on its morphology. This study expands the literature on this owl's basic biology by providing a larger set of morphological measurements. We captured 33 individuals and measured eight morphological variables. Additionally, we sexed the owls according to the sexing procedure of the nominate form, *A. f. flammeus*. We found that the Galápagos subspecies has shorter wings and tail but is heavier than the nominate form, with more pronounced sexual dimorphism. This study provides the most complete set of morphological data on the Galápagos short-eared owl to date, which will help to better understand its biology.

## Introduction

Insular populations of a given animal taxa often differ in body size from their continental counterparts. This phenomenon, coined the "island rule", postulates that smaller species on islands become larger over time ("insular gigantism") while larger species become smaller ("insular dwarfism") (Van Valen 1973). This may be due to shifting selection pressures for insular populations (Lomolino 2005). For example, many island species experience weaker predation pressures than their continental counterparts, so that they no longer need a smaller body to hide from predators or a larger body to actively defend against predators. Additionally, on islands larger species experience more constraints from reduced land space and resources, whereas smaller species struggle more to survive periods of food scarcity.

The **s**hort-eared owl (*Asio flammeus*) has a nearly worldwide distribution, occurring on all continents except for Australia and Antarctica. It has several isolated insular populations that are considered subspecies (Wiggins et al. 2020, Mikkola 2012). At first glance, the short-eared owl complex appears to follow the island rule, as insular subspecies have shorter wings and tails than continental subspecies (Wiggins et al. 2020, Weick 2006 Owls, Hoffmann et al. 1999, Bangs 1919, Mayr 1933). Although wing length is often used as a proxy for body size (Hamilton 1961), wing shape and length can vary according to ecological factors such as migratory behaviour or diet without a change in general body size. For example, continental short-eared owls feed mostly on small rodents (Wiggins et al. 2020, Cadena-Ortiz et al. 2019, Cirignoli et al. 2001), whereas insular owls prey on a higher proportion of birds (de Groot 1982, Wang 2022). For this reason, Amadon (1943) advocated using body mass as a proxy for body size if whole-body measurement is not possible (Rising and Somers 1989). However, published data on body mass across short-eared owl subspecies – except *A. f. flammeus* – is sparse (but see Weick 2006).

Female short-eared owls are slightly heavier and larger than males (Scherzinger and Mebs 2020, Wiggins et al. 2020). In the nominate subspecies, *A. f. flammeus,* both sexes have similar plumage, except that males are brighter (Scherzinger and Mebs 2020, Demongin 2016) and have less strongly barred inner webs on secondaries 1–4 and tail feather 6 (Demonging 2016). It is not known if these differences also occur in other short-eared owl subspecies.

The Galápagos short-eared owl, an endemic subspecies of the short-eared owl, feeds on small native prey such as moths (*Manduca* spp.), lava lizards (*Microlophus* spp.), and a variety of bird species, as well as invasive rats (*Rattus rattus*) and mice (*Mus musculus*) (De Groot

1982). Here, we report the most complete set of morphological measurements taken to date in wild Galápagos short-eared owls (*Asio flammeus galapagoensis*). Additionally, we sexed the owls based on their plumage coloration and morphological features. The aim of this study was to expand our knowledge on the basic biology of this island endemic.

## Methods

### Study site and species

This study was conducted on Floreana Island (1°17′51″S 90°26′03″W) and Santa Cruz Island (0° 38′ 0″ S, 90° 21′ 0″ W) in the Galápagos Archipelago, Ecuador. Floreana Island has an area of about 173 km² and Santa Cruz Island 986 km². The islands' vegetation has been subdivided into six zones: 1) the littoral zone at the sea's edge, dominated by shrubs and small trees like the red mangrove (*Rhizophaga mangle*) and *Lycium minimum*; 2) the arid zone (elevation 80–300 m), dominated by arborescent and shrubby species of *Opuntia*, *Jasminocereus* and *Brachycereus* cacti; 3) the transition zone, which covers a large part of the islands and is dominated by a mix of evergreen and deciduous plants like the palo santo tree (*Bursera graveolens*) or *Croton scouleri*; 4) the *Scalesia* zone, whose trees can reach heights of 20 m or more, occurring at elevations from 180–550 m. The three tree genera *Scalesia, Psidium* and *Pisonia* characterize this zone; 5) the *Miconia* zone, occurring on Santa Cruz Island at elevations of 400–550 m, where rainfall diminishes, and soil becomes more acidic. This zone is characterized by more or less dense shrubbery of *Miconia robinsoniana, Baccharis, Darwiniothamnus* and other species; and 6) the fern-sedge zone, occurring on Santa Cruz Island at elevations of 500–700m, dominated by ferns and sedges. The dominant species are sedges of the genera *Cyperus*, *Eleocharis* and *Scleria*. The tallest plants of that zone are the tree ferns *Cyathea weatherbyana,* which has fronds of 2–3 m length (Wiggins and Porter 1971).

Floreana has around 130 permanent human residents, while Santa Cruz has about 15,700 (INEC 2015). On both islands, the majority of the human population live in coastal villages. The remaining inhabitants live in the highlands, mostly on farms. Most of the islands' surface is protected as part of the Galápagos National Park; nevertheless, about 8% of Floreana island's surface and 14% of Santa Cruz island's surface have been altered by humans. On both islands, the highland humid zones have been most degraded by human activity, affecting 38% of the highlands on Floreana Island and 88% on Santa Cruz Island (Watson et al. 2009).

**Capture and processing of owls**

From 27 January–17 March 2023, we captured 33 short-eared owls using a noose on a pole (29 individuals) or a bal-chatri trap (4 individuals; Berger and Mueller 1959). The noose on a pole consisted of three 1-m-long hollow metal tubes mounted together, through which we passed an elastic cord (0.8 mm thick) that formed a noose at one end. Once an owl was seen on the road, perched on a small fence post, or a lower branch of a tree, one experimenter (SCS) carefully approached the owl up to a distance of 2–3 m and placed the noose over its head. An assistant (JP or JC) stood 3–5 m to one side and distracted the owl by making noises. They then secured the owl as soon as the noose closed around its neck. Due to the cord's size and elasticity, it was possible to capture the owls without causing injury. We placed a metal band containing a unique alphanumerical ID and a unique combination of two coloured plastic rings on the owl's tarsi and measured eight morphological variables: tarsus length (from joint between tarsus and toes to intertarsal joint, in mm), tarsus width (mm), wing length (mm), tail length (mm), head length (mm), head width (mm), bill length (tip to head in mm) and body mass (g) (Demongin 2016). The wing feathers of three owls and the tail feathers of four were broken, so no associated measurements were taken. The owls were

sexed based on their plumage patterns (Fig. 1) (Demongin 2016). We initially determined sex during handling (performed by PS and SCS) and later blindly confirmed this assignation based on photographs taken during capture (performed by PS). Mean ± SE time in captivity per owl was 55.9 ± 1.75 min (range 37–85 min), whereas the active handling time (measurements, taking a blood sample and putting the harness on) never exceeded 60min.

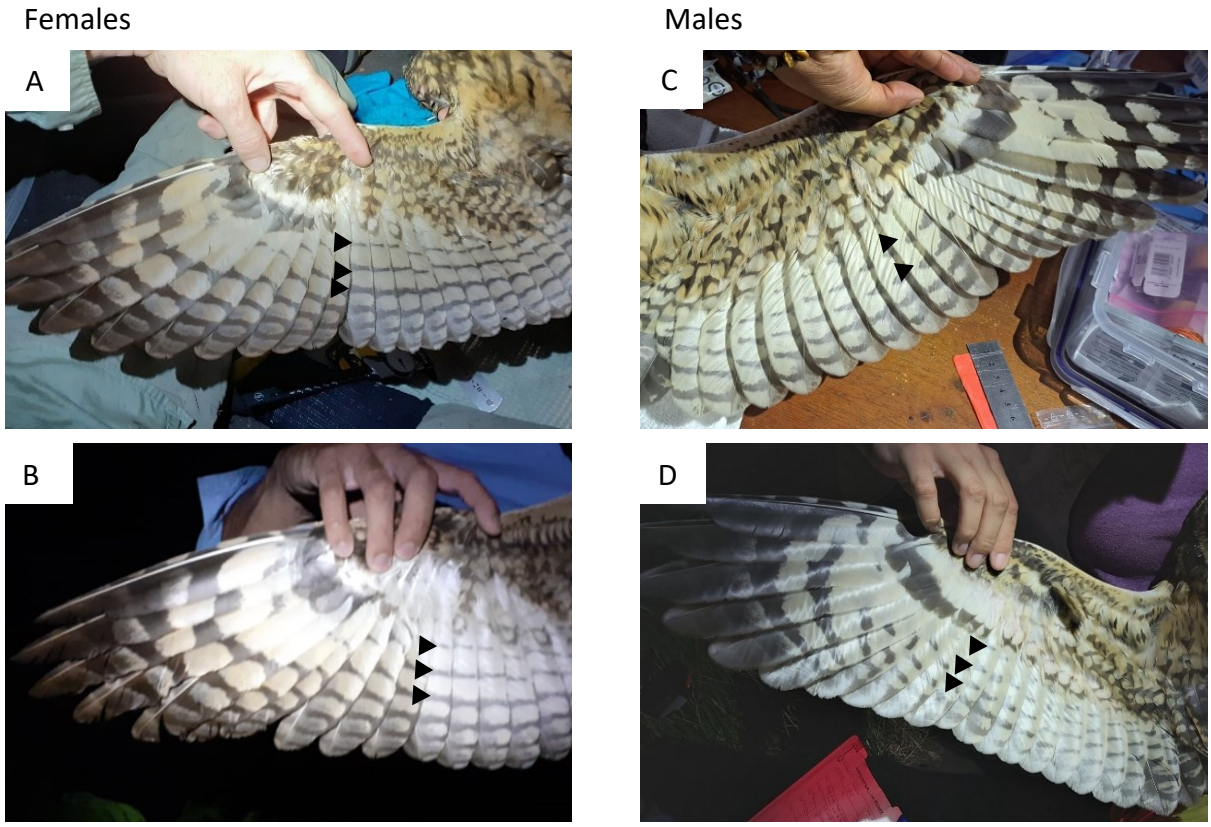


Figure 1: Photographs of the inner wing pattern of four Galápagos short eared owls (*Asio flammeus galapagoensis*). Panels A–B show two females and C–D two males. The upper dark bars of secondaries 1–4 reach the edge in females but not in males (black arrows).

**Statistical analysis**

All statistical analysis were performed with R v. 4.2.2 (R Core Team 2023) and Excel version 2305 Build 16501.20210. Morphological differences between sexes were tested using unpaired t-tests assuming homoscedasticity.

**Ethical note**

Permission to conduct this study was granted by the Galápagos National Park Directorate (DPNG) (PC-89-22). All owls were handled by or under supervision by two professional and experienced raptor banders (PS and SCS) to minimize stress and risk of injury. No owl suffered any obvious injury from being handled. The owls were released at their site of capture within 90 mins and we found no obvious negative impact on the owl's health over the following nights.

## Results

Our sample comprised 21 females and 12 males. Sex assigned in the field generally agreed with sex based on photographs, with only three exceptions. Sexing based on photographs best matched the relationship between mass:head length (Fig. 2).

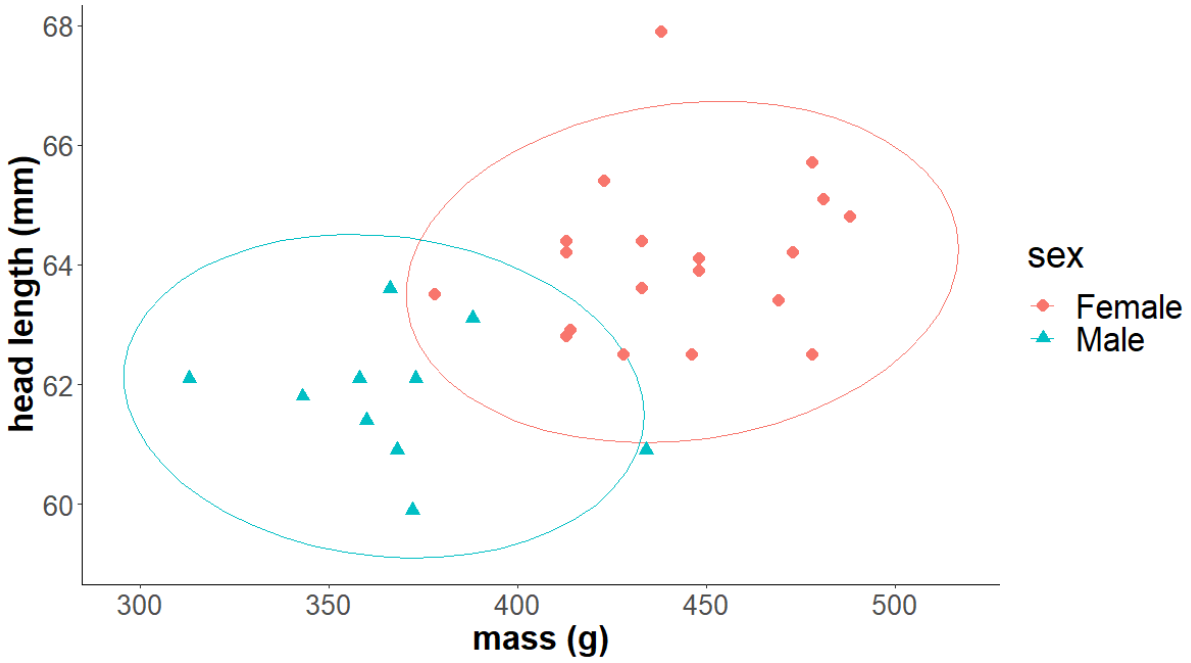


Figure 2: Differences between sexes in the mass:head length relationship, as indicated with a cluster plot with 95% confidence ellipses.

Summary values of the population for each morphological variable are given in Table 1 and grouped by sex in Table 2. On average, females were heavier than males, had longer wings, a longer head, a longer tail, a longer bill, and wider tarsi (all $p < 0.02$; Table 3). Sexes did not significantly differ in tarsus length or head width (Tables 2, 3).

Table 1: Eight morphological measurements of the Galápagos short-eared owl (*Asio flammeus galapagoensis*). All measurements were taken following standard procedures described by Demongin (2016). Three owls had broken wing feathers and four had broken tail feathers, so no respective measurements could be taken in these cases.

| Variable | Mean | SE | Range | N |
|---|---|---|---|---|
| mass (g) | 413.8 | 8.6 | 313.0–488.0 | 33 |
| wing length (mm) | 298.6 | 1.6 | 271.0–310.0 | 30 |
| head length (mm) | 63.3 | 0.3 | 59.9–67.9 | 33 |
| head width (mm) | 45.1 | 0.3 | 41.0–50.7 | 33 |
| tail length (mm) | 141.9 | 0.8 | 133.0–155.0 | 29 |
| bill length (mm) | 31.39 | 0.2 | 29.7–33.3 | 33 |
| tarsus length (mm) | 48.5 | 0.5 | 41.6–54.4 | 33 |
| tarsus width (mm) | 6.76 | 0.1 | 5.7–7.9 | 33 |

Table 2: Eight morphological measurements of the Galápagos short-eared owl (*Asio flammeus galapagoensis*) grouped by sex. All measurements were taken following standard procedures described by Demongin (2016). Three owls had broken wing feathers and four had broken tail feathers, so no respective measurements could be taken in these cases.

| | Females | | | | Males | | | |
|---|---|---|---|---|---|---|---|---|
| | Mean | SE | Range | N | Mean | SE | Range | N |
| mass (g) | 443.1 | 6.5 | 378.0–488.0 | 21 | 362.3 | 8.8 | 313.0–434.0 | 12 |
| wing length (mm) | 301.6 | 1.4 | 282.0–310.0 | 21 | 291.4 | 3.4 | 271.0–302.0 | 9 |
| head length (mm) | 64.1 | 0.3 | 62.5–67.9 | 21 | 61.8 | 0.3 | 59.9–63.6 | 12 |
| head width (mm) | 45.24 | 0.3 | 42.5–47.4 | 21 | 44.8 | 0.7 | 41.1–50.7 | 12 |
| tail length (mm) | 143.3 | 1.0 | 135.0–155.0 | 20 | 138.7 | 1.3 | 133.0–.143.0 | 9 |
| bill length (mm) | 31.7 | 0.2 | 29.9–33.3 | 21 | 30.9 | 0.2 | 29.7–32.5 | 12 |
| tarsus length (mm) | 49.0 | 0.7 | 41.6–54.4 | 21 | 43.3 | 0.6 | 43.3–50.3 | 12 |
| tarsus width (mm) | 6.2 | 0.1 | 6.2–7.9 | 21 | 6.5 | 0.1 | 5.7–7.2 | 12 |

Table 3: Results of t-tests comparing eight morphological measurements of the Galápagos short-eared owl (*Asio flammeus galapagoensis*) between sexes. Significant results are highlighted in bold.

| | t-value | df | p-value |
|---|---|---|---|
| mass (g) | 7.46 | 31 | **< 0.001** |
| wing length (mm) | 3.33 | 28 | **0.002** |
| head length (mm) | 4.97 | 31 | **<0.001** |
| head width (mm) | 0.67 | 31 | 0.505 |
| tail length (mm) | 2.89 | 27 | **0.008** |
| bill length (mm) | 2.47 | 31 | **0.019** |
| tarsus length (mm) | 1.29 | 31 | 0.207 |
| tarsus width (mm) | 2.90 | 31 | **0.007** |

## Discussion

The Galápagos short-eared owl is an understudied subspecies, with most literature to date focusing on the species' feeding habits (Harris 1970, Abs et al. 1975, de Groot 1982, Iudica 2019), ecology and conservation status (de Groot 1982, Dvorak 2017), and genetics (Schulwitz et al. 2019). Studies of the subspecies' morphology are scant (Gould 1837, Schulwitz et al. 2019) and no data have been published on their head dimensions, mass, or sexual dimorphism in terms of size or plumage patterns. Tarsus measures between studies are often not comparable due to differences in measurement method, with some researchers reporting total tarsus length (e.g., Schulwitz et al. 2019) and others measuring the tarsus bone length (i.e., to the intertarsal joint, as in this study).

In this study, we followed the standardized procedures described in Demongin (2016). Our measurements could form the basis for future research on this subspecies' morphology, which could lead to a better understanding of its ecology and evolution. The Galápagos subspecies does show some differences from *A. f. flammeus* (Cramp et al. 1989, Fünfstück and Weiß 2018, Mikkola 2012, Wiggins et al. 2020), having a shorter wing length (Cramp et al. 1989, Fünfstück and Weiß 2018, Mikkola 2012, but see Wiggings et al. 2020) and tail length (Cramp et al. 1989, Wiggings et al. 2020), but a larger bill and tarsus length (Cramp et

al. 1989) and a heavier mass (Earhart and Johnson 1970, Clark 1975, Cramp et al. 1989, Wiggins et al. 2020, but see Fünfstück and Weiß 2018). Hence, our data suggest that the Galápagos short-eared owl does not consistently follow the "island rule", as the reduced wing and tail length would indicate insular dwarfism whereas the increase in mass hints at insular gigantism. Meiri et al. (2004, 2006) postulated that the island rule does not hold true for island mammalian carnivores because they do not experience strong predation pressure, but no general analysis has been conducted for birds of prey. In the Galápagos short-eared owl, two possibilities may account for the reduction in wing and tail length. Firstly, the nominate subspecies is migratory (Wiggins et al. 2020) and known for distant dispersal (Calladine et al. 2024), whereas the Galápagos population is resident and undertakes only short-distance inter-island movements (Grant et al. 1975, Schulwitz et al. 2019). Insular populations of migratory species that have lost their migratory activity tend to have shorter wings because long-distance flight is no longer required (Fitzpatrick 1998). Secondly, the Galápagos short-eared owl historically fed mainly on birds, with invasive rodents added to their diet only in the last 300 years (Abs et al. 1965, De Groot 1982, Harper and Carrion 2011), whereas the continental subspecies mainly prey on rodents (Clark 1975, Cramp 1989, Cadena-Ortiz et al. 2019, Restrepo-Cardona et al. 2021). Capturing avian prey requires more agility, whereby shorter, rounded, and more elliptical wings might lead to more successful hunts (Lockwood et al. 1998; Corvidae et al. 2006). These two factors may have led to the reduction in wing and tail length in the Galápagos short-eared owl without a general reduction of body size. A more thorough analysis into wing loadings and comparison of their wing shape might provide better insights.

To sex Galápagos short-eared owls, we used morphological markers based on descriptions by Demongin (2016). The Galápagos subspecies is considerably darker than other subspecies

(Gould 1837) and in no individuals did we observe an unbarred inner web on the secondary wing feathers or an unbarred outer web on the tail feathers, as would be expected in males (Demongin 2016). Nevertheless, the description that secondary feathers have "dark bars not reaching the edge" in males and "dark bars reaching the edge" in females (Demonging 2016, p. 196) was helpful for determining sex in this subspecies. Specifically, males had bars that reached the edge – but only the two outermost bars – on their first four secondaries, while females had 4–5 bars reaching the edge. With these results, we are confident that morphometric parameters alone can provide a reliable estimate of sex. Future research should use genetic sexing techniques to confirm the accuracy of these morphology-based methods.

Female Galápagos short-eared owls were heavier than males and had greater wing length, head length, tail length, bill length, and tarsus width (bill to head), but did not differ from males in their tarsus length and head width. Reversed sexual dimorphism (RSD), where the female is larger than the male, is common in birds of prey and is most pronounced in raptors and owls that hunt fast-moving and agile prey, such as birds (Snyder and Wiley 1976, Newton 1979, Krüger 2005, Andersson and Norberg 1981). It is noteworthy that females of the Galápagos subspecies were significantly larger in six of the eight morphometric variables we measured, while *A. f. flammeus* does not show strong RSD. In the nominate subspecies, RSD in wing length has variously been reported as non-existent (Earhart and Johnson 1970, Lundberg 1986) and moderate (Mueller 1986), although all three studies found clear RSD in body mass (Earhart and Johnson 1970, Lundberg 1986, Mueller 1986). Tail length and tarsus length did not differ between sexes, whereas RSD was moderate for beak depth and strong for foot size (not measured in our study) and beak length (Mueller 1986). Several hypotheses have been proposed to explain RSD in owls: (1) reproductive role division, (2) sexual selection, and (3) intersexual food competition. The latter hypothesis has received the most

attention but has generally not been supported by research findings (Korpimäki 1981, Lundberg 1986, Mueller 1986, but see Pande and Dahanukar 2012). Because the Galápagos short-eared owl hunts a significantly higher proportion of avian prey biomass than its continental counterparts (50.8% vs 0–8%; de Groot 1982, Cadena-Ortiz et al. 2019, Restrepo-Cardona et al. 2021), its smaller body and shorter wings may have evolved to improve hunting efficiency. The difference in tarsus width, but not length, might also indicate a sex-dependent division of prey items (i.e. females within a breeding pair hunt larger prey than males), as seen in other species (Panter & Amar 2021). However, further research on the hunting behaviour of male and female short-eared owls is needed to test this hypothesis. If males and females target different-sized prey, the resulting expansion of the dietary niche within the breeding pair could improve reproductive success (Solis and Guttiérrez 1990, Tate et al. 2016). Overall, short-eared owls divide their intersexual roles during reproduction, with the male providing most of the prey for the female and offspring, while the female performs most of the incubation, brooding, and nest guarding. Sexual size dimorphism might have further advantages (Newton 1979). Successful reproduction depends on the body condition of the female (Hirons 1985). Lundberg (1986) proposed that RSD in owls might stem from the fact that larger females are more resistant to bad weather conditions and epochs of food scarcity. Populations of Darwin's finches – the owls' main prey item – heavily depend on seasonal rainfall and can collapse during dry years (Boag and Grant 1986), making them an unpredictable food source. Heavier females would be better equipped to breed in dry years, whereas lighter females would have to forego breeding. Hence, for the Galápagos short-eared owl, becoming smaller and lighter may allow more efficient hunting of avian prey but a trade-off might exist for incubating females, leading to more pronounced RSD.

Here, we provide the most complete set of morphological data on the endangered short-eared owl subspecies of the Galápagos islands. The Galápagos subspecies has shorter wings and tail, but is slightly heavier, so no clear trend in overall body size change was found. Contrary to the nominate form, we found clear evidence for sexual dimorphism, whereby females were larger than males in six out of eight measurements. We also attempted to sex owls in the field. While we are confident that we sexed the individuals correctly, genetic sexing techniques will ultimately provide a more definitive answer.

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# Chapter 2: Evidence for personality in Galápagos short-eared owls (*Asio flammeus galapagoensis*): cross-context behavioural response


## Abstract

Animal personality can have profound effects on inter- and intraspecific interactions and hence shape community structure. To date, we know little about personality in raptor species that play a key role in trophic system regulation. In this study, we measured personality traits in the Galápagos short-eared owl *(Asio flammeus galapagoensis)*, with the aim to test consistency across contexts. We measured the association between behavioural response on the boldness axis (number of struggles during handling) and, several days or weeks later, as flight initiation distance (FID) upon approach. On the aggressiveness axis, we measured owls' response to a mirror (mirror stimulation test) and to playback of conspecific calls. In 19 wild owls tested on Floreana and Santa Cruz Islands during 2023 and 2024, we found the expected consistency across contexts on the boldness axis: birds that struggled more during handling had closer shorter flight initiation distances during FID tests. During the playback trials we found a significant difference in the number of gazes between treatment and control. As well as a near significant difference in the latency to first gaze towards the stimulus. On the other hand, no difference between treatment and control was found in the number of head movements. No cross-context correlation (mirror stimulation test and conspecific playback) was found in the number of gazes and latency to gaze but a strong positive correlation between playback and mirror treatment in the number of head movements. This study uses new rapid field assessment techniques for personality in owls and finds support for consistency in boldness and aggressiveness across contexts in the Galápagos short-eared owl.

## Introduction

Understanding species- and individual-level differences in populations of keystone species can improve our understanding of their role in ecosystems (Sergio et al. 2008, Kovács et al. 2008). Keystone species have a disproportionately large influence on trophic interactions (Bond 1994) and their presence or absence can trigger dramatic trophic cascades, despite their relatively low abundances (Brown and Heske 1990, Paine et al. 1985). For example, the reintroduction of wolves (*Canus lupus*) to Yellowstone National Park excluded elk (*Cervus canadensis*) from certain areas, reducing the foraging pressure on aspen that were suffering due to the unnaturally large elk population (Fortin et al. 2005) and after sea otters (*Enhydra lutris*) disappeared from sites around the Aleutian Archipelago sea urchin populations grew strongly, which consequently reduced the density of sea kelp forests and caused shifts in fish populations (Reisewitz et al. 2005).

Personality traits are inter-individual differences in behavioural response norms to prevailing external conditions (i.e., social, ecological) that are consistent across time and contexts (Sih et al. 2004, Réale et al. 2007. Five broad, non-overlapping behavioural axes are commonly used to study animal personality: (1) the boldness-shyness axis quantifies response to risky, non-novel situations, (2) the aggressiveness axis quantifies agonistic response to a conspecific, (3) the activity axis quantifies an animal's general level of activity, (4) the exploration-avoidance axis quantifies response to novel situations, and (5) the sociability axis quantifies affiliative response towards conspecifics (Réale et al. 2007). These traits have been tested across vertebrate and invertebrate taxa (for a review see: Laskowski et al. 2022) and have been shown to be associated with individuals' life history (e.g. slow versus fast pace of life) and fitness (Dingemanse & Réale 2005, Wolf & Weissing 2012, Smith & Blumstein 2008).). Generally, there are two criteria for establishing evidence of a personality trait: first, the behavioural response norms must be repeatable over time, and, second, there should be

individual consistency in behaviour across contexts. While most individual-level repeated behavioural tests have been conducted in captivity (MacKinley and Shaw 2022), there are a growing number of field studies (McCowan et al. 2015, Bilby et al. 2022, Herborn et al. 2010). In the field, it may not always be possible to repeat measurements across time when animals are difficult to re-trap or re-sight; in such cases, it is especially important to validate the response profile across contexts (e.g. in-hand versus free-moving in the wild).

Different methodologies have been used over the years to better understand animal personality. Of the five commonly studied personality axes, boldness has been most studied (Kaiser & Mueller 2021), albeit with some inconsistencies in terminology and methodology. Although Réale et al. (2007) explicitly excluded novelty from their definition of 'boldness', various authors have measured boldness as the latency to enter a novel environment (Chapman et al. 2011), or to approach a novel object (Wilson et al. 1994). Presenting the focal individual with a predator (Cavalli et al. 2016, Müller & Juškauskas 2018) excludes novelty and, hence, satisfies this definition of boldness. Because many wild animals regard humans as a potential predator, boldness is often measured as individuals' response to being handled by a human (Bilby et al. 2022) and/or flight initiation distance (FID) in response to an approaching human (Uchida et al. 2019, Luna et al. 2020). Aggressiveness has been measured as an individual's agonistic response towards its mirror image (Colombelli-Negrel et al. 2022), the broadcast of conspecific vocalisations (Da Silva et al. 2013), and/or the physical presence of a conspecific (Michelangeli et al. 2017). Both boldness and aggressiveness have been linked to different ecologically relevant traits, whereby bolder and more aggressive birds have been shown to have greater reproductive success (Réale et al. 2000, Tamin et al. 2023), faster growth rates (Ward et al. 2004, Mondal et al. 2005), and longer dispersal distances (Michelangeli et al. 2017, Duckworth 2008). In some species, the

covariation between boldness and aggressiveness has been described as forming a behavioural syndrome along the proactive-reactive axis, with proactive individuals tending to be bold and aggressive and reactive individuals tending to be shy and non-aggressive (Sih et al. 2004, Tamin et al. 2023).

Personality traits have been most extensively tested in a few model systems, such as great tits (*Parus major*) (Dingemanse et al. 2002, Dingemanse et al. 2003) and chimpanzees (*Pan troglodytes*) (Massen et al. 2013, Pederson et al. 2005), whereas the majority of taxa, like owls, are underrepresented in personality research. Only a handful of studies have attempted to quantify personality traits in this group (van der Brink et al. 2012, Peleg et al. 2014, Da Silva et al. 2013, Luna et al. 2019). While these studies measured the repeatability of behaviour across time, to date only two studies have compared behavioural response across contexts in owls (Carrete and Tella 2017, Cavalli et al. 2016). While investigating the effects of urbanisation on burrowing owls *(Athene cunicularia*), latency to approach a model predator and distance to flee from an approaching human covaried in a rural population but not in an urban population (Carrete and Tella 2017). On the other hand, rural owls reacted similarly to a human approaching alone and one approaching with a dog, while urban owls reacted more strongly towards the human with a dog (Cavalli et al. 2016).

The Galapagos short-eared owl (*Asio flammeus galapagoensis*) is a keystone species on Floreana Island in the Galapagos Archipelago. It is the last remaining native large predator on this island after the Galapagos hawk (*Buteo galapagoensis*) and the Galapagos barn owl (*Tyto alba punctatissima*) have been extirpated by humans (Steadman and DeLeon 1999) and the only remaining natural predator of invasive rats and mice (de Groot 1982, Cadena-Ortiz et al. 2019). Slight changes in its foraging behaviour could have great effects on a lower trophic

level. Certain personality traits are linked with foraging efficiency and/or niche exploitation, then the composition of traits within a predator population may have important consequences for ecosystem function. In dragonflies (*Epitheca canis*), populations with more active larvae were more effective in hunting zooplankton, which led to different prey community composition and higher algae density (Start & Gilbert 2017).

The aim of this study was to test whether Galapagos short-eared owls show consistency in individual-level response patterns across contexts for boldness and aggressiveness in the wild. Although no study to date has quantified personality traits in this subspecies, we made use of established methods that have been used successfully in other owl species. As measures of boldness, we recorded the number of struggles during handling (Peleg et al. 2014) and flight initiation distance (Carrete and Tella 2010). As measures of aggressiveness, we recorded the owls' response to the broadcast of conspecific vocalisations (Luna et al. 2019, Da Silva et al. 2013) and to mirror-image stimulation. While the response to a mirror stimulation test has not been used in owls to date, this is a well-established method to test for aggressiveness in other bird species (Bilby et al. 2022, Schuett et al. 2011) and was trialled here in a nocturnal species. We predicted that 1) handling response and flight initiation distance would be positively associated (cross-context consistency for boldness); and 2) mirror response and playback response would be positively associated (cross-context consistency for aggressiveness).

## Methods

### Study site and species

The Galápagos short-eared owl is a Galápagos endemic subspecies of the short-eared owl (*Asio flammeus*). The only other raptor species on the archipelago are the Galápagos barn owl

(*Tyto alba punctatissima*) and the Galápagos hawk (*Buteo galapagoensis*) – both of which are not present on the island of Floreana and only the barn owl is also present on Santa Cruz. Galápagos short-eared owls feed on small prey such as moths (*Manduca* spp.), lava lizards (*Microlophus sp.*), rats (*Rattus rattus*), mice (*Mus musculus*) and a variety of bird species (De Groot 1982). Most bird species on the Galápagos islands tend to show high tolerance towards humans, possibly because of the lack of native mammalian predators. We captured short-eared owls on Floreana Island from February–March 2023 (N = 31) and in March 2024 (N = 2), and on Santa Cruz Island in January 2023 (N = 1) and January 2024 (N = 1).

**Capture and processing of owls**

Most owls (N = 31) were captured using a noose on a pole. The pole consisted of three 1-m long hollow metal tubes mounted together, through which we passed an elastic cord (2 cm thick) that formed a noose at one end. After locating an owl perched on the road, small fence post, or lower branch of a tree, one experimenter (SS) carefully approached the owl up to 2–3 m and placed the noose over its head. The cord's size and elasticity made it possible to capture the owls without causing injury. A second experimenter (JP or Jonathan Cueva) stood 3–5 m to one side and distracted the owl by making noises—for example by rubbing a shoe on the road. After the noose closed around the neck of the owl, the second researcher (JP or Jonathan Cueva) secured the owl by grabbing its body and holding its wings tight to reduce the chance of injury. In four cases, owls were captured using a bal-chatri trap (Berger and Mueller 1959) with moths or rodents as bait. After capture, the owls were ringed using one metal ring with unique alphanumerical ID and a unique combination of two coloured plastic rings. Additionally, we took a blood sample (400 µl) and the following morphological measurements: tarsus length and width, wing length, tail length, head length and width, bill length (bill to head), and body mass (Demongin 2016). The owls were being processed

(ringing, morphometrics, blood sampling and harnessing with GPS logger) for a maximum of 60min, while the time in captivity (handling time) was longer (mean ± SE duration of 59 ± 2 min, range 37–89 min).

**Personality assays**

We conducted four behavioural assays along two personality axes: boldness (number of struggles in hand when held by a human, flight initiation distance when approached by a human) and aggressiveness (response to conspecific playback and to mirror-image stimulation), hereafter referred to as "conspecific playback trial" and "mirror trial". In addition, we used two control trials (broadcast of cow vocalizations, exposure to the non-reflective back of the mirror) to test if the owls reacted differently to the treatment trials, hereafter referred to as 'control playback' and 'mirror control'. The order of assays was randomized, and the control and treatment trials were completed either on the same night or on different nights. Trials were conducted from February to March 2023, during July 2023, in January 2024, and in March 2024. We tested 33 owls for their struggles, 19 for their FID, 28 for their reaction to a conspecific playback, and 18 for their reaction to a control playback, 16 for their reaction towards a mirror and 14 for their reaction towards the back of a mirror (described below). The different sample sizes stem from the opportunistic nature of data collection of wild individuals. During that time struggles and FID were conducted by multiple researchers (JP, SS, PS, SK), whereas the other trials only by one (JP) except the trials done in 2024. Three conspecific playback trial were conducted by JP in July 2023, six conspecific playback trials and control playback trials were conducted and filmed from February to March 2024 by ACK and then scored by JP. Two struggles and FID trials were conducted in February and March 2024 by SS.

**Boldness**

We used two different behavioural assays to measure boldness in wild owls. In our first assay we measured boldness as the number of struggles during handling (mean ± SE handling time = 58 ± 2 min, range 37–85 min). A "struggle" was defined as a forceful burst of uninterrupted movement (Peleg et al. 2014, Bilby et al. 2022). The 31 owls were handled by four different researcher (PS, SS, JP, JC) and handler ID had no significant effect on the number of struggles (ANOVA: $F = 1.515$, $df = 3$ $p = 0.233$). In our second assay we measured boldness as the flight initiation distance (FID) on any consecutive night a banded owl was first resighted. FID has been used in a variety of species (Møller 2009) and shown to be highly repeatable across years in burrowing owls (*Athene cunicularia*) (Carrete and Tella 2010, Carrete and Tella 2013). We followed the protocol by Blumstein (2006): the observer noted the distance (~ 20m) towards the focal individual (never perched higher than 2 m) and started walking at a constant pace of ~1m/s and then noted the distance at which the bird flew away. We tested 21 owls (8 males, 11 females, two of unknown sex). Of these, 14 were tested by JP, 6 by SS, and one by SK.

**Aggressiveness**

We used two different behavioural assays to measure aggressiveness in wild owls. We measured aggressiveness as the behavioural response to conspecific playback in 28 owls (6 males, 13 females, 9 of unknown sex). Most owls (N = 19) were colour-banded and previously ringed in early 2023. The others (N = 9) were not banded and tested in July 2023 or Spring 2024. We exposed each owl to three minutes of broadcast of the call of a short-eared owl (recordings from 5 different owls) recorded from Floreana and Santa Cruz Island during the previous three years by Paula Castaño. The control stimulus was cow vocalizations (N = 5 different cows' recordings from pixabay.com) that we tested in 18 owls (8 males and 4 females, 6 of unknown sex). For the conspecific stimulus file, we broadcast a call every 2-3 s for 3 min and for the cow stimulus file, we broadcast a call every 10 s for 3min. During

playback, the speaker (MIFA WildCamping) was positioned on the ground about 10 m from the owl. The observer (JP or ACK) observed the owls from about 10 m away, perpendicular to the speaker, using binoculars and illuminating the owls with a headtorch just enough for them to be visible. We measured the response of the focal owl as: number of head movements (continuous head movement in any direction), gazes towards the speaker (looking into the direction of the speaker), and latency (s) to first gaze towards the speaker. If an individual kept looking into the direction of the speaker for more than 5 s we added one count of "gaze". This accounts for the fact that when owls hear a sound of interest they tend to lock into the direction of the source (Ohayon et al. 2006, Takahashi 2010). Originally, we accounted also for approach distance and vocalization (da Silva et al. 2013), but no owl vocalized and only two approached the speaker and none the mirror.

We measured aggressiveness as the response to a mirror in the field. The sample size was 16 owls (7 males and 9 females). A human observer (JP) placed the mirror (round, 40 cm in diameter) around 5 m in front of the focal individual. With two exceptions (perched on 5-m-high pole and 4-m-high branch), the owls were either standing on the ground or perched at a maximum height of 1.5 m. Because data collection happened at night, artificial lighting was used to ensure that the owls could see the mirror. Specifically, in nine cases a nearby streetlight provided enough lighting, in five cases the light source of the speaker (MIFA WildCamping) was used to illuminate the mirror, and in two cases the owl was illuminated with the headtorch. The mirror was exposed, and the trial lasted 3 min. As with the conspecific playback trial, the response of the focal owl was measured as: number of head movements, number of gazes towards the mirror, and latency (s) to first gaze towards the mirror. For the control stimulus, we presented owls with the black, non-relfective back of the mirror in 14 owls (7 males and 7 females) and measured their response as above. As with the

playback assay, if an individual kept looking into the direction of the mirror for more than 5 s, we added one count of "gaze".

**Statistical analysis**

All statistical analysis were performed with R v. 4.2.2 (R Core Team 2023) and Excel version 2305 Build 16501.20210. Linear mixed models (LMMs) and generalised linear mixed models (GLMMs) were performed using R package lme4 v. 1.1.31 (Bates et al. 2015).

*Boldness*

We conducted Pearson's correlation tests to assess the association between our two boldness variables (struggles and FID). Because of the big difference in the time in captivity between the owls we used a Pearson's correlation to examine the relationship between total struggles and struggles per minute. Both measurements correlated strongly with another (Pearson: $r^2 = 0.76$, $p < 0.001$, $n = 31$), so we used the total number of struggles thereafter and did not control for time in captivity.

*Aggressiveness*

For the conspecific playback assay, we tested for differences in response to treatment and control trials using two LMMs with number of head movements and number of gazes, respectively, as the response variable. Both models included stimulus type (conspecific, cow) as a fixed effect and BirdID as a random effect. For the mirror assay, we tested for differences in response to treatment and control trials using two LMMs with number of head movements and number of gazes, respectively, as the response variable. Both models included stimulus type (mirror, back of mirror) as a fixed effect and OwlID as a random effect.

Because of the very right-skewed distribution of the variable latency to gaze, we transformed it into a categorical variable with two levels: slow (owl took more than 5 s to look towards the stimulus) and fast (owl took less than 5 s to look towards the stimulus). We then used a GLMM with the same effects to test for the difference between treatment and control trials. To test the relationship between our two aggressiveness variables, we used two Pearson's correlation tests to compare subjects' number of head movements and number of gazes, respectively, between the playback trial and mirror trial. To ensure that the expected correlation only occurred in response to the intended stimuli, we repeated these correlation tests to compare subjects' number of head movements and number of gazes, respectively, between the control playback trial and control mirror trial.

### Ethical note

Permission to conduct this study was granted by the Galápagos National Park Directorate (DPNG) (PC-89-22). All owls were handled by or under supervision by two professional and experienced raptor banders (PS and SCS) to minimize stress and risk of injury. No owl suffered any obvious injury from being handled. The owls were released at their site of capture within 90 mins, and we found no obvious negative impact on the owl's health over the following nights.

## Results

### Boldness

The mean ± SE number of struggles during handling was 27.4 ± 1.7 (range 12–47, n = 33) and mean ± SE flight initiation distance was 1.7 ± 0.23 m (range 0.55–5.00 m, n = 21). There was no difference between sexes in the number of struggles ($t(29) = -0.735$, $p = 0.469$) nor between sexes in FID ($t(17) = -1.079$, $p = 0.300$). Our cross-context comparison of boldness

scores showed a statistically significant association: birds that struggled more during handling also had a shorter FID (Pearson $r^2 = 0.20$, $p = 0.040$, $n = 21$) (Fig. 1).

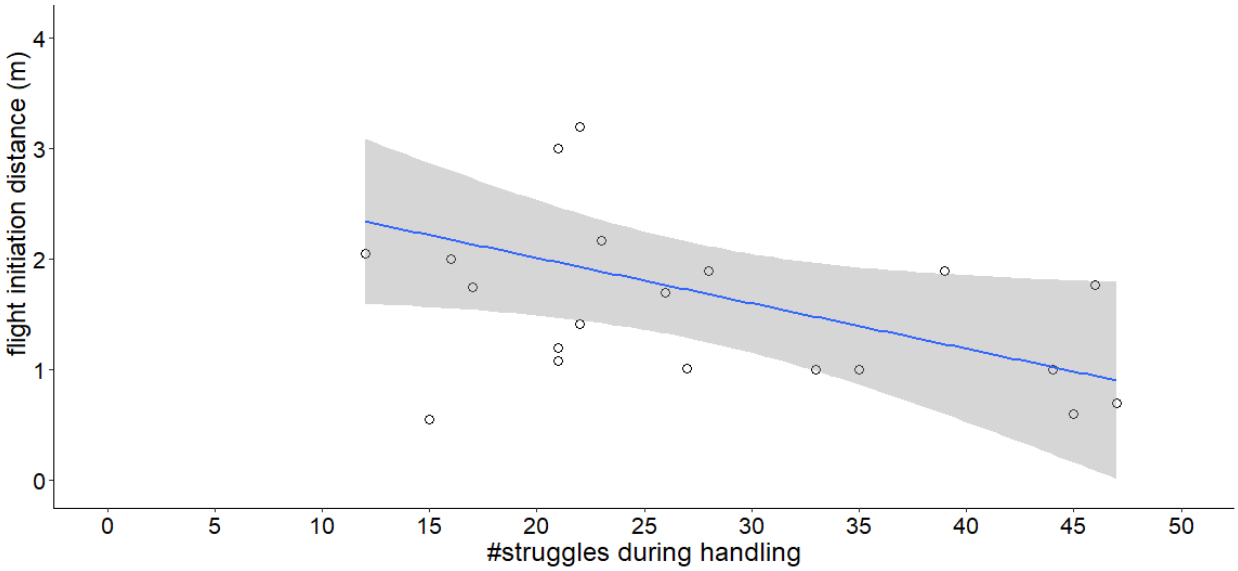


Figure 1: The significant association between two boldness measurements across contexts (number of struggles, flight initiation distance) in 21 short-eared owls. Birds that struggled more when held by a human tended to have a shorter flight initiation distance when approached by a human (see results). Pearson $r^2 = 0.20$, $p = 0.040$, $n = 21$

**Aggressiveness**

During the playback trials, owls gazes more often towards the stimulus than during the control trials, but did not show a significant difference in the number of head movements (Fig. 2, Tab. 1). Similarly, during the mirror trials owls did not respond differently towards the treatment (reflection in the mirror) than towards the control (back of the mirror) (Fig. 3, Tab. 1). There was a near significant trend to gaze quicker towards the conspecific playback than towards the cow playback (Table 2).

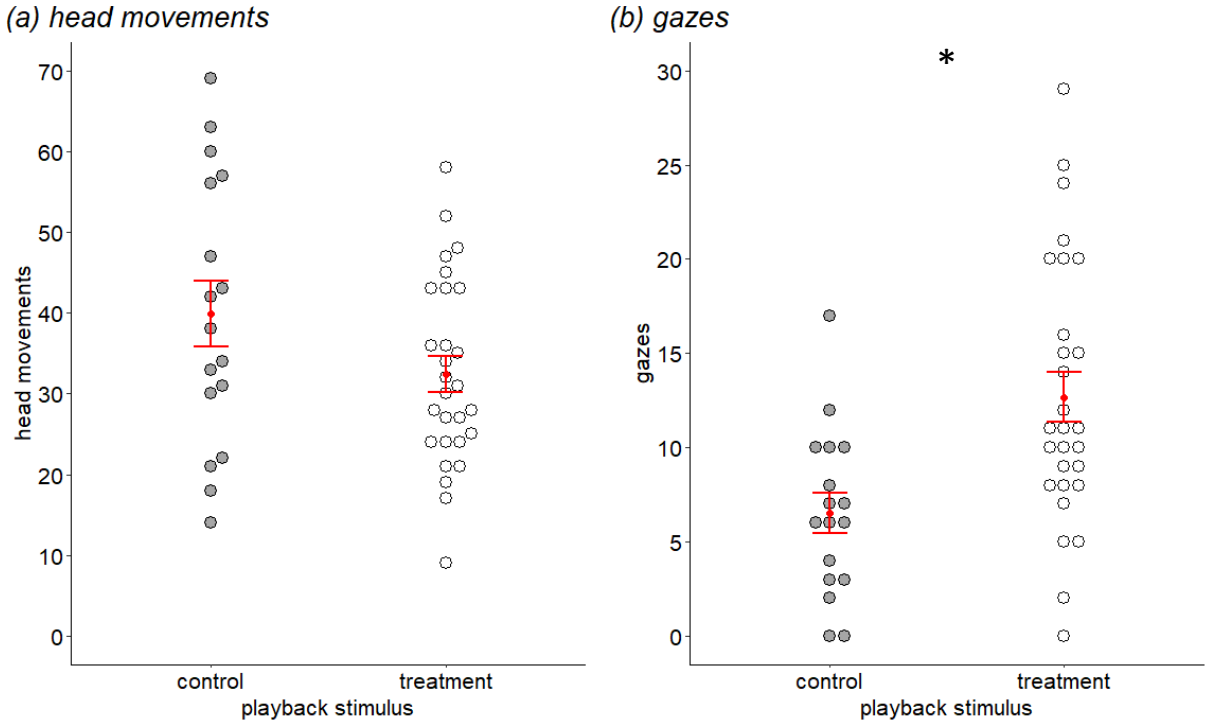


Figure 2: a) head movements (continuous head movements in any direction) and b) gazes (looks towards the stimulus) made by Galápagos short-eared owls during the playback stimulus (treatment vs control). Treatment: conspecific call every 2-3 s during 3 min. Control: cow call every 10 s during 3 min. N(control playback_head movements) = 18, n(control playback_gazes) = 17, n(Treatment) = 28

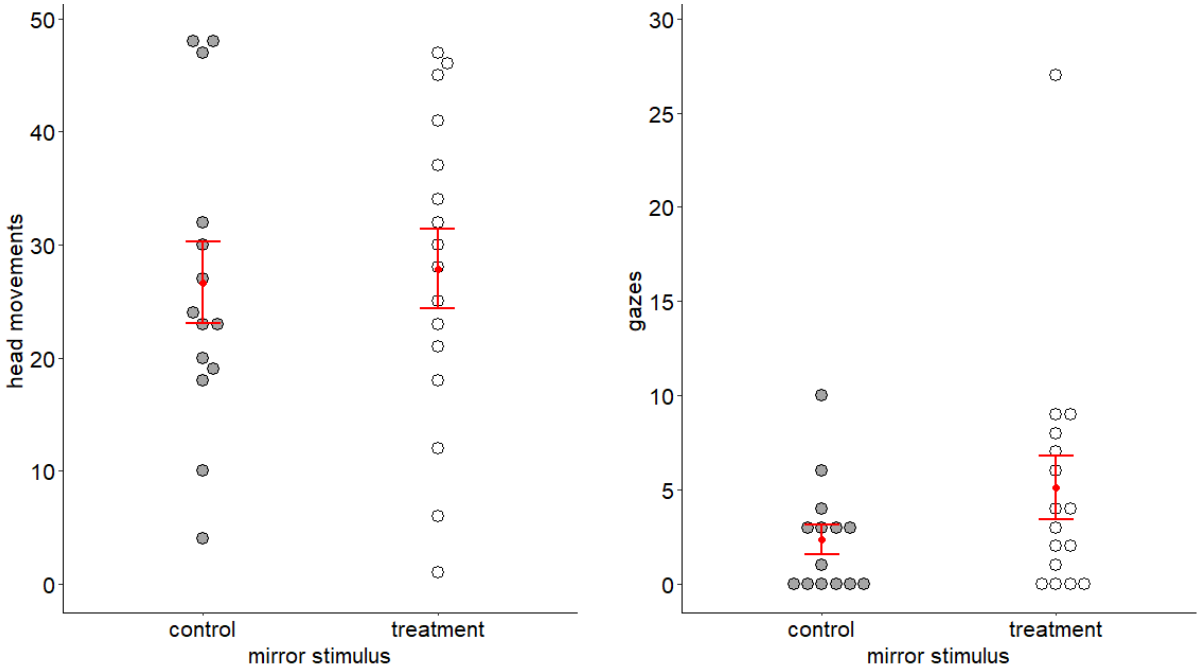


Figure 3: Differences of number of a) head movements (continuous head movements in any direction) and b) gazes (looking towards the stimulus) made by Galápagos short-eared owls during the mirror stimulus (control vs treatment). N(control) = 14, n(treatment) = 16.

Table 1: Output from LMMs testing whether there is a difference between treatment (conspecific playback or mirror) and control (cow playback or unreflective back of mirror) trials in the number of head movements (continuous head movement in any direction) and gazes (looks towards the stimulus) made by Galapagos short-eared owls.
Trial type (treatment or control) was entered as fixed factor and ID as random effect. Model a tested for the difference of head movements in the playback trials. Model b tested for the difference of gazes in the playback trials. Model c tested for the difference of head movements in the mirror trials and model d tested for the differences of gazes in the mirror trials.

| Fixed effects | Estimate | Std. Error | t | P | N |
|---|---|---|---|---|---|
| a) Playback head movements | | | | | |
| Intercept | 38.435 | 3.181 | 12.082 | < 0.001 | 18 |
| Trial type | -6.042 | 3.568 | -1.694 | 0.103 | 18 |
| b) Playback gazes | | | | | |
| Intercept | 7.074 | 1.500 | 4.715 | < 0.001 | 17 |
| Trial type | 5.605 | 1.730 | 3.240 | 0.005 | 17 |
| c) Mirror head movements | | | | | |
| Intercept | 26.712 | 3.660 | 7.298 | < 0.001 | 14 |
| Trial type | 1.163 | 4.455 | 0.261 | 0.798 | 14 |
| d) Mirror gazes | | | | | |
| Intercept | 2.357 | 1.411 | 1.670 | 0.106 | 14 |
| Trial type | 2.768 | 1.933 | 1.432 | 0.163 | 14 |

Table 2: Output from GLMMs testing whether there is a difference between treatment and control trials in the of latency to first gaze towards stimulus made within the first 5 s of the trials and after 5 s made by Galapagos short-eared owls.
Trial type (treatment or control) was included as fixed effect and ID as random effect. Model 5 tested for the difference in the latency in the playback trials and model 6 tested for the difference in the latency in the mirror trials.

| Fixed effects | Estimate | Std. Error | z | P | N |
|---|---|---|---|---|---|
| a) Playback | | | | | |
| Intercept | -0.082 | 0.624 | -0.132 | 0.051 | 17 |
| Trial type | 2.059 | 1.057 | 1.949 | 0.051 | 17 |
| b) Mirror | | | | | |
| Trial type | -2.137 | 1.138 | -1.878 | 0.060 | 14 |
| Mirror trials | 1.146 | 1.056 | 1.084 | 0.278 | 14 |

There was a strong positive association between the number of head movements during the playback trial and the mirror trial ($r(14) = 0.674$, $p = 0.004$), but no association between the control playback trial and the control mirror trial ($r(9) = 0.371$, $p = 0.262$). No association was found between the number of gazes during the playback trial and the mirror trial ($r(14) = -0.103$, $p = 0.705$), nor between the control playback trial and the control mirror trial ($r(9) = 0.393$, $p = 0.231$) (Fig. 4, Fig. 5).

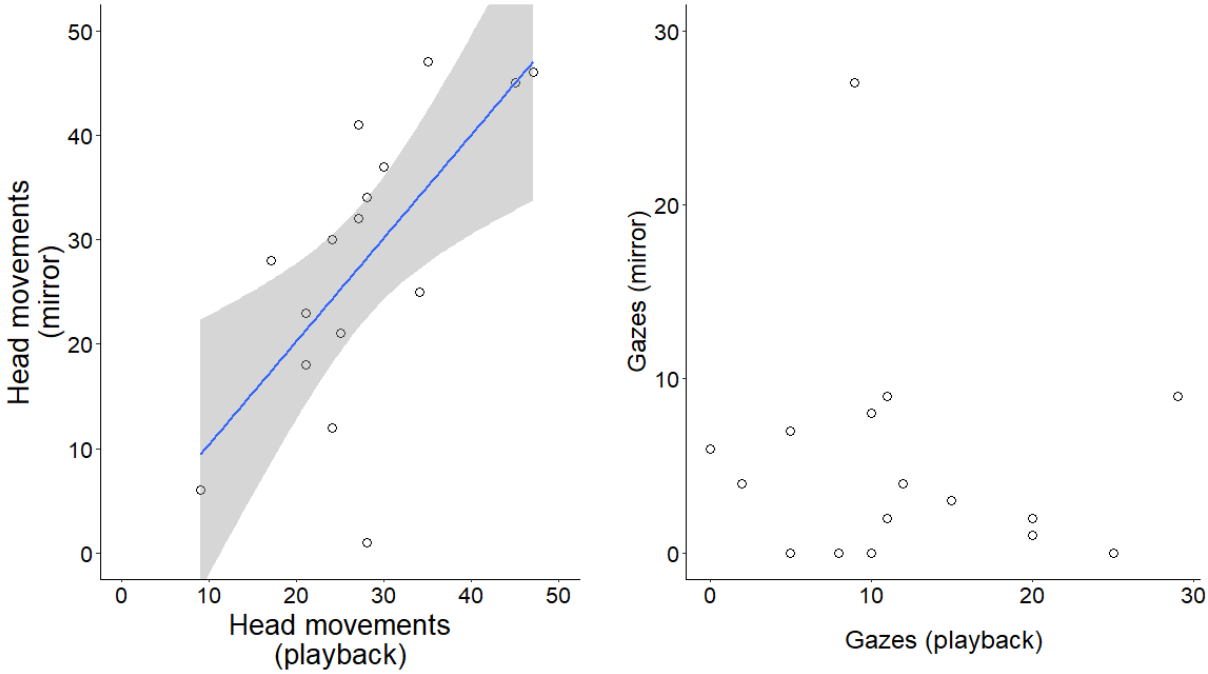


Figure 4: Scatterplot showing the correlation between number of head movements (continuous head movement in any direction) and gazes (looks towards the stimulus) by Galápagos short-eared owls during both treatment trials (playback and mirror). A strong positive association was found for the number of head movements ($r(14) = 0.674$, $p = 0.004$) but not for the number of gazes ($r(14) = -0.103$, $p = 0.705$).

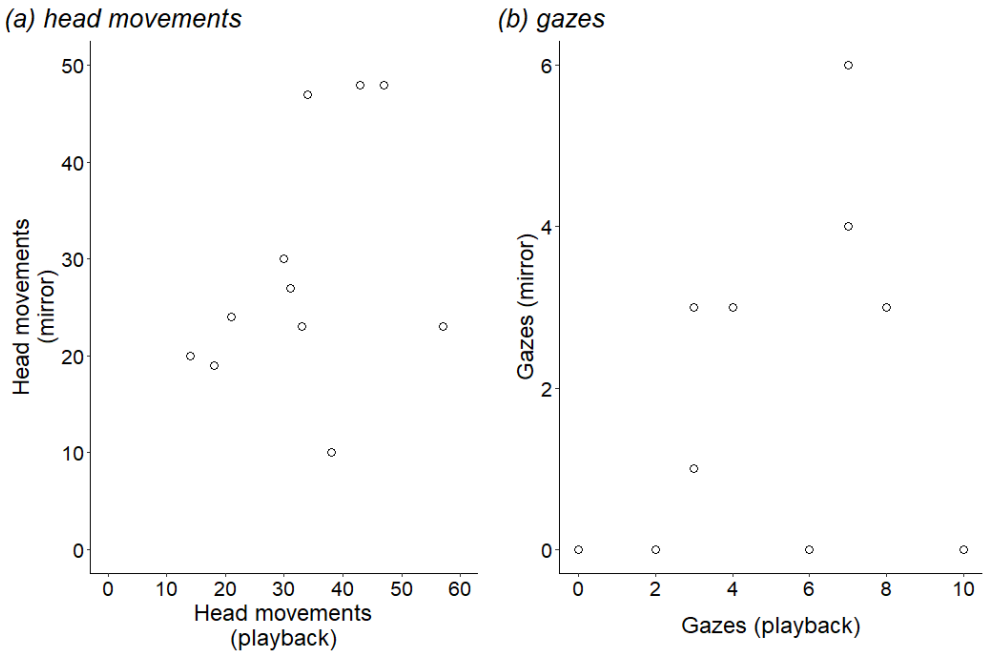


Figure 5: Scatterplot showing the correlation between number of head movements (continuous head movement in any direction) and gazes (looks towards the stimulus) made by Galápagos short-eared owls during both control trials (playback and mirror). No association was found for the number of head movements ($r(9) = 0.371$, $p = 0.262$) nor for the number of gazes ($r(9) = 0.393$, $p = 0.231$).

## Discussion

In this study, we compared individual behavioural response across two contexts using behavioural tests that have been validated as personality traits with individual repeatability in other studies (Carrete and Tella 2013, Petelle et al. 2013, da Silva et al. 2013, Bilby et al. 2022), namely number of struggles during handling, FID, response to conspecific playback, and mirror stimulation. Our two measures of boldness correlated with each other, with owls that struggled more during handling (high boldness) also fleeing at shorter distances from an approaching human (high boldness). In our aggressiveness measures we found no difference between control and treatment stimulus in the mirror trials, but we did find one in the playback trials. The owls showed more gazes and showed a trend towards having shorter latency to first gaze towards the stimulus in the conspecific playback trials. We found a positive association between an individual owl's number of head movements when exposed to a conspecific playback and to its mirror image.

Our two measures of boldness correlated with each other, with owls that struggled more during handling also exhibiting shorter flight initiation distances. This suggests that boldness is consistent across experimental contexts in this species. In previous research, FID and latency to approach a predator model were correlated (Cavalli et al. 2016) but no study has tested these response variables against number of struggles during handling. While no correlation between FID and handling struggles was found in yellow-bellied marmots (*Marmota flaviventris*) (Petelle et al. 2013), there was a clear and strong pattern of association in yellow-spotted monitors (*Varanus panoptes*) (Ward-Fear et al, 2018). Handling struggles were negatively correlated with the frequency of trapping in bighorn sheep (*Ovis canadensis*) (Réale et al. 2009). In burrowing owls (*Athene cunicularia*), the correlation between FID from an approaching human and latency to approach a perceived predator (Carrete and Tella 2017) or FID from an approaching human with a dog (Cavalli et al. 2016)

depended on if the owls were from an urban or rural environment. In rural owls, both boldness measurements correlated, while they did not in urban owls. Our results indicate that FID and struggles during handling might both lie on the boldness axis in the Galápagos short-eared owl and are both strategies to mitigate risky situations. We acknowledge that we did not measure temporal repeatability for either variable, since owls were seldom resighted or recaught, despite our efforts to do so. However, repeatability for both variables has been shown in other owl systems (Carrete and Tella 2013, van den Brink et al. 2012). This is the first study to test for an association between handling struggles and FID, and finds the expected correlation, supporting the cross-context validation of these two variables as measures of the boldness personality axis.

Our two measures of aggressiveness (playback and mirror treatment) on a populational level did only differ from the control trials in the number of gazes during the playback trials. The owls gazed more often towards the stimulus during the conspecific playback trial than during the control trials. When an owl hears a sound of interest, it quickly turns its head towards the source. If it decides that the sound is of interest (conspecific, prey), the owl locks into that direction to locate the position of the source of the sound (Ohayon et al. 2006, Takahashi 2010). Although owls gazed towards the conspecific playback more often than the cow playback, their reaction was weaker than anticipated (Da Silva et al. 2013, Galeotti et al. 2024), because no owls vocalized and only two approached and attacked the speaker. We know very little about the vocal repertoire of the Galápagos short-eared owl. Thus, we do not know the function of the call type we used for the conspecific playback trial. Nevertheless, we think that the playback elicited an aggressive response in the owls as two individuals ended up attacking the speaker. Thus, individuals that showed higher interest in the playback probably did that because they were more aggressive (da Silva et al. 2013). We found no

difference in the behavioural responses between treatment and control during the mirror trials. Lighting conditions were not standardised thus some individuals may not have seen the mirror properly. It could also be the case that a uniquely visual cue is not enough to trigger an aggressive response in this subspecies. Future work should aim to further assess if a mirror elicits a mirror-specific response from an owl under standardised conditions.

We found a strong positive correlation between the number of head movements during the conspecific playback trial and the mirror treatment trial. Overall, the number of head movements is considered an arousal response in owls (Masino & Knudsen 1993, Ohayon et al. 2006). At the population level, we had comparable number of head movements across all four stimulus groups, with some owls being highly aroused with many head movements to any stimulus, including the control stimuli. The number of head movements was only correlated at an individual level between the conspecific playback and the mirror treatment, and not with any control test or between control tests, lending some support to the idea that there is cross-context consistency in arousal at the individual level when responding to a conspecific playback or to their mirror-image.

As with the boldness variables, we do not have individual repeatability for either variable as owls were only seen on two different nights (in two cases, on three nights), including the night of capture. Future research should aim to test the repeatability of individual responses to conspecific playback (Da Silva et al. 2013). Although the consistency of mirror response has not been demonstrated in owls, this trait has been shown to be repeatable in other birds, including greylag geese (*Answer answer*) (Kleindorfer et al., 2024) and superb fairywrens (*Malurus cyaneus*), but this information is lacking for owls. Future work should aim to further explore arousal and its measurement in owls, including how aggressive responses

change over time based on season or reproductive phase. While we discovered one active nest with two owlets during the study period in July 2023, it is not clear how synchronous the breeding season is for the Galapagos short-eared owl, for example. In general, the owls seemed to be quite social as up to eight individuals were observed in an approximately 0.5 $km^2$ area at the same time (personal observation).

In this study, we first tested short-eared owls for behavioural differences in traits associated with boldness and aggressiveness across contexts in the wild. For our measures of boldness, we found the expected negative correlation between FID and number of struggles during handling. For our measurements of aggressiveness, we found the expected positive correlation between the number of head movements to trials and no such association in any other combination with control trials. While owls reacted more strongly towards the conspecific playback trials than towards the control playback trials, we found no such difference when comparing the mirror trial and control mirror, raising questions about the validity of the mirror test. But a clear and strong correlation was found between both treatment trials (conspecific playback and mirror) in the number of head movements. Overall, our results support the existence of measurable personality traits in this subspecies with the caveat that we need more research into mirror tests in owls. Future research should focus on testing the repeatability of behaviour in owls, as well as using rapid field assessment tests across contexts to measure personality in raptors more widely.

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## Supplementary Material

Table S1: Mean, SE, range and sample size of the number of head movements (continuous head movement in any direction) and gazes (looks towards the stimulus) made by Galapagos short-eared owls during 3 min of trials: playback treatment (call of conspecific every 2–3 s), control playback (call of cow every 10 s), mirror treatment (round mirror 40 cm in diameter placed 5 m from the focal individual) and control mirror (black back of the mirror placed 5 m from the focal individual).

| **Playback trial** | Mean | SE | Range | n |
|---|---|---|---|---|
| Head movements | 32.39 | 2.19 | 9-58 | 28 |
| Gazes | 12.68 | 1.34 | 0-29 | 28 |
| **Playback control** | | | | |
| Head movements | 38.94 | 3.94 | 14-69 | 18 |
| Gazes | 6.53 | 1.08 | 0-17 | 17 |
| **Mirror trial treatment** | | | | |
| Head movements | 27.88 | 3.50 | 1-47 | 16 |
| Gazes | 5.13 | 1.67 | 0-27 | 16 |
| **Mirror trial control** | | | | |
| Head movements | 26.64 | 3.61 | 4-48 | 14 |
| Gazes | 2.36 | 0.78 | 0-10 | 14 |

Table S2: Percentage of latency to first gaze towards stimulus made within the first 5 s of the trials and after 5 s made by Galápagos short-eared owls during 3 min of trials: Mirror treatment (round mirror 40 cm in diameter placed 5 m from the focal individual), control mirror (black non-reflective back of the mirror placed 5 m from the focal individual, playback treatment (call of conspecific every 2–3 s) and control playback (call of cow every 10 s).

| **Latency to gaze** | % 0-5s | % 6-180s | N |
|---|---|---|---|
| Mirror stimulus | 27% | 73% | 15 |
| Control Mirror | 14.3% | 85.7% | 14 |
| Playback stimulus | 82.6% | 17.4% | 23 |
| Control playback | 47.1% | 52.9% | 17 |

# Chapter 3: Personality and movement behaviour in Galápagos short-eared owls (*Asio flammeus galapagoensis*)


## Abstract

Understanding how animal personality links to individual movement in space in keystone species is of great importance for conservation management. The Galápagos short-eared owl (*Asio flammeus galapagoensis*) is the only endemic large terrestrial predator on Floreana Island in the Galápagos Islands, Ecuador. Although movement, space use, and personality have been studied separately in owls, little research to date examined the association between these traits and none in relation to home range. The aim of this study is to close this knowledge gap by measuring owls' personality traits and correlating them with utilization distribution, a proxy for home range that describes the probability of an animal occurring at a certain location in space. We captured 31 short-eared owls and tagged them with GPS loggers to determine their utilization distribution on Floreana Island. In addition, we measured two behavioural traits (boldness and activity) in wild owls, using both experimental and observational methods. There was a significant correlation between our two behavioural variables ascribed to boldness (flight initiation distance and struggles during handling), and a strong correlation between three activity variables measured using landscape-level movement data. Additionally the three activity variables were highly repeatable over time. Utilization distribution differed between sexes but was not correlated with any of our behavioural traits. These results could help inform conservation decisions for these island predators, particularly those involving the eradication of invasive prey, translocation, and capture-and-release programmes. This study provides further insight into personality differences in an understudied taxa and is the first to examine the possible link between personality and utilization distribution in any owl species.

## Introduction

Understanding the factors influencing animal movement is a crucial step towards understanding ecosystem functioning, as the presence or absence of certain species can have cascading effects throughout the food web (Paine 1966). In particular, apex predators have a major influence on their ecosystems (Bond 1994, Fortin et al. 2005). For example, the disappearance of sea otters (*Enhydra lutris*) from sites around the Aleutian Archipelago led to a rise in sea urchin populations, which in turn reduced the density of sea kelp forests and caused shifts in fish populations (Reisewitz et al. 2005). In addition, the healthy coexistence of predators with their prey can result in the phenomenon known as "predator-prey space race" (Sih 1984). This occurs when prey species attempt to reduce spatial overlap while predators strive to maximise shared space (Suraci et al. 2022). Other factors known to influence an animal's movement include sex (Cederlund and Sand 1994), age (Grüss et al. 2011) and breeding status (Mack and Clark 2006). Another factor known to shape the spatial movement of animals is personality (Wat et al. 2020, Eccard et al. 2022, Ward-Fear et al. 2018).

Every animal has a distinctive response to the same external stimuli. When individuals' reactions are consistently different across time and contexts, these differences are defined as personality traits (Sih et al. 2004, Réale et al. 2007). Five main behavioural axes are typically used to represent different personality traits: (1) the boldness-shyness axis quantifies response to risky, non-novel situations, (2) the exploration-avoidance axis quantifies response to novel situations, (3) the activity axis quantifies an animal's general level of movement, (4) the aggressiveness axis quantifies agonistic responses towards conspecifics, and (5) the sociability axis quantifies affiliative responses towards conspecifics (Réale et al. 2007). These traits are present throughout the animal kingdom (reviewed by Laskowski et al. 2022). They are heritable to a certain degree (Sinn et al. 2006) and may be stable both within (Katsis

et al. 2023) and across (Wuerz and Krüger 2015) life stages. Moreover, personality traits have been demonstrated to influence an individuals' life history and fitness (Dingemanse & Réale 2005, Wolf & Weissing 2012, Biro & Stamps 2008, Smith & Blumstein 2008). Furthermore, the repeatability of personality traits can vary depending on the sex and taxon in question (Bell et al. 2009, Debeffe et al. 2015).

One of the most commonly used metrics for measuring spatial movement is home range, which quantifies the area that an animal typically utilizes to fulfil its daily activities of food gathering, mating, and caring for young (Burt, 1943). If only shorter tracking periods are available that, for instance, do not include breeding and non-breeding season, the space used by an individual does not fit the definition of a home range. In such instances, the term "utilization distribution" (UD) is a more precise fit, as it describes space use as a probability distribution (Powell & Mitchell, 2012). If the location-time series underlying the UD become long enough and incorporates different stages in the annual or life cycle, a UD can fulfil the criteria to be termed home range. An animal's home range size is driven by external factors such as weather (Rivrud et al. 2010), food sources (Corriale et al. 2013), seasonal changes (Quirici et al. 2010) and landscape changes (Bartlam-Brooks et al. 2013), as well as internal factors such as group size and composition (Wang et al. 2011), sex (Sprogis et al. 2016) and age (Cederlund and Sand 1994). With the rise of global positioning systems (GPS), it has become possible to pinpoint location-time series of animal movement with increasing accuracy (Cagnacci et al. 2010, Nathan et al. 2022).

The personality of an animal can influence the size of its home range. For example, bolder animals may be more inclined to exploit riskier areas of habitat, whereas more exploratory animals may be more likely to investigate new areas of habitat, and more active animals may

simply be able to cover larger areas, thereby increasing their home range size (Spiegel et al. 2017). This theory has been supported by a number of empirical studies. For example, in monitor lizards (*Varanus panoptes*) and bank voles (*Myodes glareolus*), bold individuals had larger home ranges than their shyer counterparts (Ward-Fear et al. 2018, Schirmer et al. 2019). Similarly, more exploratory starlings (*Sturnus vulgaris*) had larger home ranges than their less exploratory conspecifics (Minderman et al. 2010). In common brushtail possums (*Trichosurus vulpecula*), the relationship between home range size and personality was sex dependent. Specifically, more exploratory males had larger home range sizes and more exploratory females had smaller home ranges (Wat et al. 2020). Nevertheless, it is possible that these patterns are species-specific and may not be applicable to other systems (Laskowski et al. 2015, Underhill et al. 2021).

As owls often occupy ecological niches that no other species do, they can impose strong selection pressures on their prey (Marti 1987). Screech owls (*Megascops* spp.), for example, preferred to prey on smaller individuals of the same mouse species (Marti and Hogue 1979), and deer mice (*Peromyscus maniculatus*) changed their behaviour according to the moonlight's intensity to modulate predation risk by short-eared owls (*Asio flammeus*) (Clark 1983). Thus, it is important to study which factors influence an owl's movements, as these can directly affect their prey. To date, home range size in owls has been linked with habitat selection (Glenn et al. 2004), foraging prey type (Zabel et al. 1995), breeding success and sex (Séchaud et al. 2021). For example, female barn owls (*Tyto alba*) and eagle owls (*Bubo bubo*) had larger home ranges than males (Séchaud et al. 2021, Campioni et al. 2013). Other types of movement such as dispersal and migration has also been shown to be influenced by sex in other owl species (Forsman et al. 2002, Catlin 2004, Beckett and Proudfoot 2012). But differences between sexes themselves can depend on the reproduction cycle (Sunde et al.

2003) and habitat (Redpath 1995). The number of studies examining the relationship between personality and spatial movement in owls is limited, with the majority of research focusing on breeding dispersal patterns (Luna et al. 2019; 2020). However, to our knowledge, no study to date has investigated the potential link between personality and home range. Three studies have reported substantial inter-individual variation in movement and home range in eagle owls (*Bubo bubo*) and barn owls (*Tyto alba*), respectively. Nevertheless, despite the authors' acknowledgement of personality as a potential influencing factor, no actual testing was conducted (Campioni et al. 2013; 2016, Cain et al. 2023).

The aim of this study was to test whether Galápagos short-eared owls (*A. f. galapagoensis*), an island-endemic subspecies of the short-eared owl, show consistency in individual-level response patterns across contexts for boldness and activity in the wild, and how these personality traits correlate with their utilization distribution and what effect sex has on all variables. Specifically, we measured boldness as (1) the number of struggles during human handling, and as (2) flight initiation distance (FID) in response to an approaching human. We measured activity based on three measurements of locomotion activity (referred to as "activity") extracted from GPS-logger data (maximum distance travelled, net square displacement, and diffusion rate). We predicted that (1) handling response and FID would be negatively associated (i.e. high number of struggles and low FID would both indicate a bold phenotype); and (2) all three measures of activity would be positively correlated and show intra-individual repeatability over time, indicating a personality trait along the activity axis, (3) individuals' boldness and activity would be positively correlated with their utilization distribution size and (4) females will have a larger home range size than males.

## Methods

### Study site and species

We conducted this study on Floreana Island (1°17′51″S 90°26′03″W) in the Galápagos Islands, Ecuador, which has a total area of 173 km². The island's vegetation is separated into three distinct zones as the climate gets wetter with increasing altitude: dry zone (0–200/300 m), transition zone (200/300–400 m), and humid zone (300–640 m), with different vegetation types dominant per zone (Watson et al. 2009, Dvorak et al. 2017, Aurelio Simbaña Ayo 2023). The lowlands sustain arid-adapted plants such as *Opuntia echos* cacti, acacia (e.g. *Acacia macrantha*), and palo santo trees (*Bursera graveolens*); the transition zone is a mix of acacia, palo santo, and shrubs, including Darwin's cotton (*Gossypium darwinii*); and the highlands are dominated by *Scalesia pedunculata* and cat's claw (*Zanthozylum fagara*). Floreana has around 130 permanent human residents (INEC 2015). Two-thirds of this population live in the coastal village of Puerto Velasco Ibarra and the remainder live in few farms in the highlands at around 300–400m elevation. Farmland covers about 2.8 km² of the humid zone and consists mainly of agricultural crops, pasture, and small woodland plots (Dvorak et al. 2017). Only one asphalt road connects the farmlands with the village. Most of the island's surface forms part of the Galápagos National Park and is protected; nevertheless, about 8% of the island's area has been degraded by human activity, with the humid zone most strongly affected (38% degradation; Watson et al. 2009).

The Galápagos short-eared owl is an endemic subspecies of the short-eared owl. It feeds on small prey such as moths (*Manduca* spp.), lava lizards (*Microlophus* spp.), black rats (*Rattus rattus*), house mice (*Mus musculus*), and a variety of bird species (De Groot 1982). The archipelago's two other raptor species, the Galápagos barn owl (*Tyto alba punctatissima*) and Galápagos hawk (*Buteo galapagoensis*), are both absent from Floreana Island. Like most Galapagos landbirds, short-eared owls show a high tolerance towards humans, perhaps due to the lack of native mammalian predators.

**Capture and processing of owls**

We captured 31 short-eared owls on Floreana between 31 January and 17 March 2023 using either a noose on a 2–3 m long pole (27 individuals) or a bal-chatri trap with moths or rodents as bait (4 individuals) (Berger and Mueller 1959). Once the owls were safely captured, they were ringed with a metal band containing a unique alphanumerical ID and a unique combination of two coloured plastic rings for distance identification. During processing, we took a blood sample (400 µl) and eight standard morphological measurements: tarsus length and width, wing length, tail length, head length and width, bill length (tip to head) and body mass (Demongin 2016; Ploderer 2024, Chapter 1). Three owls had broken wing feathers and four had broken tail feathers (unrelated to the capture), so no measurements of these parameters were taken for these owls. We assigned sex in the field based on the owls' size and plumage patterns. These assessments were later confirmed based on systematic photographs of plumage patterns only, performed by one observer (PS) who was blind to the sex estimate from the field (Ploderer 2024, Chapter 1).

During processing, each owl was also equipped with an Ecotone GPS logger using a leg-loop harnessing method on the ALLE-300 battery units (n=9 individuals) or backpack harnessing method with degradable leather link for the ALLE-300 solar units, the CREX GPS-UHF tracker and the KITE-L GPS-UHF tracker (n=22 individuals). All loggers were equipped with a 3-mm-thick neoprene patch to elevate the tag from the feathers and to avoid skin abrasion. All harnesses were prepared with 6.5 mm wide tubular Teflon (Fig 1).

The whole processing included the ringing, morphometrics, blood sampling and harnessing with GPS logger, and did not exceed 60 min. The actual handling time per bird was longer (mean ± SE handling time 59 ± 2 min, range 37–89 min) and referred to the time between capture and release.

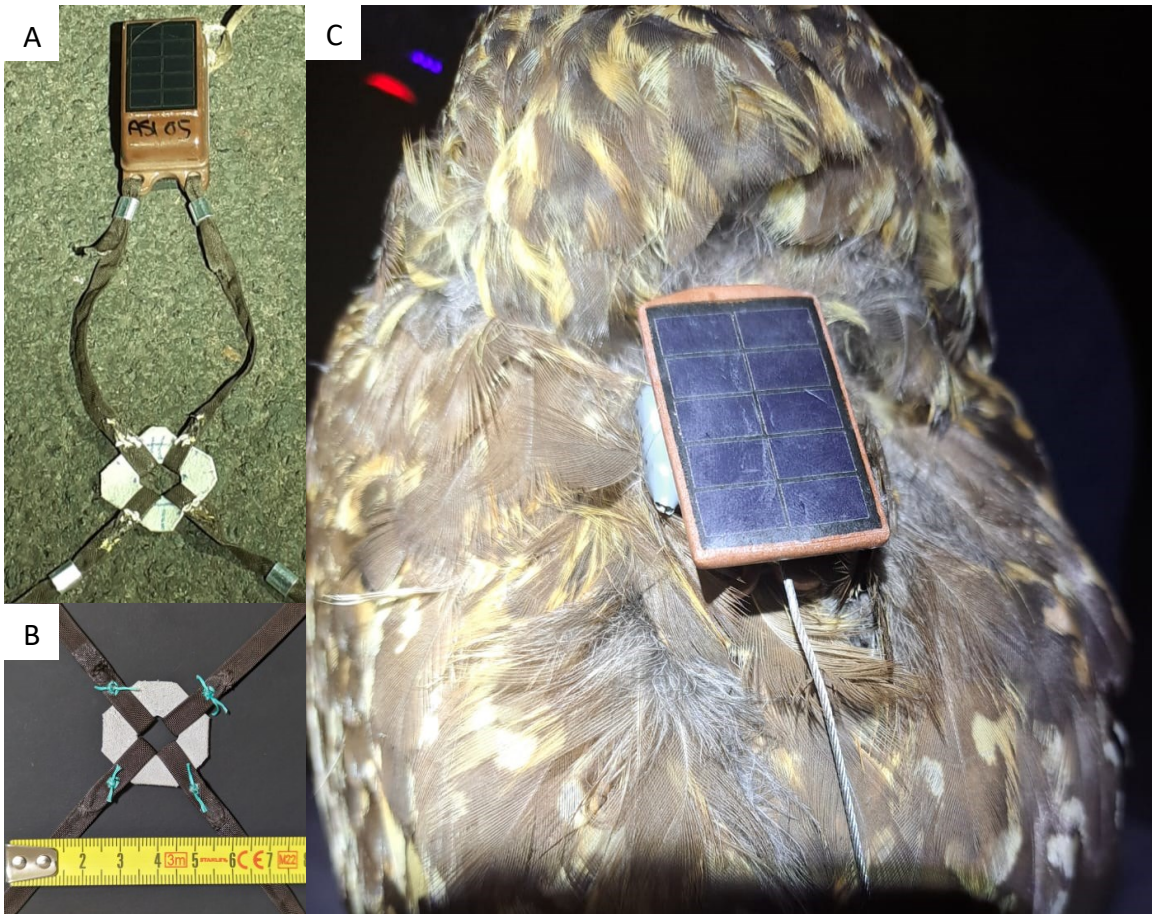


Figure 1: A: Logger before being fitted on a bird using the backpack method. B: Centre leather degradable link of the backpack method. The square is 24 × 24 mm and the centre hole is 8 × 8 mm. The Teflon straps could slide freely around the ring. The weak point of this method is the leather loop, that will eventually wear and tear off, which will permit all four straps to fall off the bird at once. C: Logger mounted on an owl. A few neck feathers were trimmed so that they did not cover the solar panel, and the logger could charge properly. Note the 1.9g VHF tag glued onto the side of the UHF-GPS tag.

**GPS sampling regime**

We used four different GPS logger models (Table 1). The first 21 owls were additionally equipped with an external VHF transmitter (Holohil 1.9g) glued with epoxy to the side of the logger. This extra unit was meant to facilitate active tracking of the owls following traditional radiotelemetry methods. However, most owls managed to reach and destroy the VHF antenna, why we stopped deploying VHF units as the added unnecessary weight with no additional data return. Galápagos short-eared owls weigh on average 435 g (females: 377–520 g, males = 260–440 g); thus, the weight of the logger plus harness and VHF unit (table 1)

never exceeded the limit of 5% considered acceptable for avian systems (Kenward 2000, Casper 2009). In addition to collecting GPS data, the CREX and KITE models also registered accelerometer (ACC) data based on three axes.

Table 1: The four different logger models used in the study. All tags logged Global positioning system (GPS) data, a subset of owls (N = 21) were additionally equipped with a VHF unit (1.9 g), and the CREX and KITE units also recorded accelerometer (ACC) data.

| Logger type | GPS + ACC | Solar panel | Mass | Harness type | N° of individuals | Total mass (with VHF) |
|---|---|---|---|---|---|---|
| ALLE 300 battery | GPS only | No | 10.5 g | Leg-loop (0.7 g) | 9 | 11.2 g |
| ALLE 300 solar | GPS only | Yes | 13.5 g | Backpack (1.2 g) | 4 | 14.7 g (16.6 g) |
| CREX GPS-UHF | GPS+ACC | Yes | 13 g | Backpack (1.2 g) | 9 | 14.2 g (16.1 g) |
| KITE-L GPS | GPS+ACC | Yes | 13 g | Backpack (1.2 g) | 9 | 14.2 g (16.1 g) |

GPS points were recorded once every hour from 4pm to 10am local time (GALT). Data were downloaded using portable Ecotone base-stations which were either positioned at elevated points on the island for several days or transported by bicycle at night. Additional data download was facilitated via a DJI Phantom 4 Quadcopter equipped with a ©Ecotone XS-UR drone base station. Efforts to download data from a logger began from the first night after the first deployment (29. Jan 2023) and ended with departure from the island (4. April 2023). During a second trip to the island from July 3rd to September 14th more efforts to downloads were made on Floreana Island and Santa Cruz Island. Data from February 1st to April 12th could be downloaded.

**Behavioural measurements, activity and movement patterns**

We conducted two behavioural assays measuring boldness in different contexts: number of struggles during handling (i.e., time between capture and release) and flight initiation distance (FID) in response to a human approach. Additionally, we extracted three different measurements of locomotion activity from the GPS data: maximum distance travelled, diffusion rate, and net square displacement (described below).

***Boldness***

For our first measure of boldness, we counted the number of struggles while the owl was handled (van den Brink et al. 2012a, Katsis et al. 2023). A struggle was defined as a forceful burst of uninterrupted movement. Because each struggle interfered with the handling procedure, owls that struggled more were also processed and handled for a longer time.

For our second measure of boldness, we measured flight initiation distance (FID) in response to a human approach. This variable has been measured across a variety of species (Møller 2009) and is highly repeatable across years in burrowing owls (*Athene cunicularia*) (Carrete and Tella 2010, Carrete and Tella 2013). Following protocols by Blumstein (2006): the observer noted the distance (~ 20m) towards the focal individual (never perched higher than 2 m) and started walking at a constant pace of ~1m/s and then noted the distance at which the bird flew away. We measured FID in 21 owls (8 males, 11 females, two unknown). Of these, 14 were tested by JP, six by SCS, and one by SK. We measured the distance (in m) at which the owl took flight (FID) using a 5-m roll meter.

***Activity***

According to Réale et al. (2007), activity represents an animal's general level of activity in a non-novel, non-risky environment. To measure this variable, we used GPS data from tagged owls to calculate three measures of locomotion activity using the R package ctmm (Version 1.1.31, Fleming and Calabrese 2023): maximum distance travelled (maximum distance between any two points per night, in m), net square displacement (straight-line distance

between the first location and the last location per night, in m) (Van de Kerk et al. 2021) and diffusion rate (the area that an animal is predicted to use on an average day in $m^2$/day) (Gill et al. 2023). We calculated maximum distance travelled by first creating a bounding box (maximum and minimum x and y coordinates per night) using the R package 'sf' (Version 1.0.9, Pebesma 2018) and then calculating the distance between the two most distant points. To quantify net squared displacement, we used the package 'sf' to calculate the squared distance between the first location and any other point (Bunnefeld et al. 2011). To calculate diffusion rate, a home range estimator was calculated using the R package 'ctmm' and the function *ctmm.select*. This function automatically calculates a diffusion rate, which was then extracted from the model. The mean values for all three activity variables per individual were then used for further analysis.

***Utilization distribution***

Utilization distribution – "the utilization distribution usually calculated shows the probabilities of where an animal might have been found at any randomly chosen time" (Powell and Mitchell 2012) – was calculated for each individual using an autocorrelated kernel density estimator (AKDE) (Fleming et al. 2015) in the package 'ctmm' (Version 1.1.31, Fleming and Calabrese 2023). This method can better deal with temporally autocorrelated data typical for animal movement. Conventional kernel density estimators (KDE) tend to underestimate animal distributions (Fleming et al. 2014), whereas AKDE does not assume identically distributed and independent data and, therefore, better projects animal home ranges, even with limited data, by taking autocorrelation into account without thinning the data or changing the sampling method (Fleming et al. 2015). After conducting model selection, the model that best explained our data was the basic AKDE Model (Silva et al. 2021). To check that all underlying assumptions were met, we visually inspected the underlying variogram, which indicates if the animal exhibited sufficiently range residency behaviour to estimate a valid AKDE, and after which sampling period the AKDE stabilises

(Fleming et al., 2014). The utilization distribution was then defined as 95% AKDE and only owls passing this quality check were included in further analysis. Two individuals (both female) flew from Floreana Island to Santa Cruz Island and back, leading to very high variation that violated the assumptions posed by AKDEs and hence made it impossible to calculate a meaningful utilization distribution (Calabrese et al. 2016). Therefore, we excluded these individuals from further movement analysis.

**Statistical analysis**

All statistical analysis were performed with R v. 4.2.2 (R Core Team 2023) and Excel version 2305 Build 16501.20210.

***Sex***

We tested the effects of sex on all parameters (boldness, activity, and utilization distribution). We used a student's t-test to test the association between sex and boldness as well as between sex and activity. When comparing utilization distribution between sexes, we used a Welch's t-test due to the lack of homogeneity of variance.

***Boldness***

To validate our "number of struggles during handling" measure, we first used a Pearson's correlation test to examine the relationship between total struggles during handling and struggles per minutes. There was a strong correlation (Pearson: $r^2 = 0.76$, $p < 0.001$, $n = 31$), why we used the total number of struggles as our variable of interest thereafter without controlling for the total handling time. Second, because the 31 owls were handled by four different researchers and handler IDs, we used an ANOVA test to confirm that handler ID had no significant effect on the number of struggles (ANOVA: $F = 1.515$, $df = 3$, $p = 0.233$).

Our two boldness measurements (number of struggles and FID) correlated strongly with each other (Pearson $r^2 = 0.20$, $p = 0.040$, $n= 21$). To obtain a single measure of boldness combining

both variables, we used a linear model (R package lme4 (Bates et al. 2015)) and fitted number of struggles as dependent variable and FID (independent variable) and extracted the residuals (hereafter referred to as ResBoldness). This variable was then tested against our measure of utilization distribution (described below).

A Rosner test from the R package 'outliers' (Version 0.15, Komsta 2022) identified two outliers in the maximum distance travelled variable, four in the net square displacement variable and four in the diffusion rate variable. After a ln-transformation of the data, these outliers were no longer apparent. All three activity measurements correlated strongly with each other (Table 2, Figure 2). Therefore, to obtain a single measure of activity per individual, we used principal component analysis (PCA) to reduce all three variables to one retained principal component (PC_Activity, see Results) with an Eigenvalue of 1.70 and explaining 96.7% of variance (R package 'stats'; R Core team 2022). Greater PC_Activity values indicated a more active behavioural phenotype: greater distance travelled per night, greater net square displacement, and higher diffusion rate.

Table 2: Correlation coefficients and p-values when comparing all three activity variables (maximum distance travelled, net square displacement, diffusion rate) with one another. N=28

| | Net square displacement | Diffusion rate |
|---|---|---|
| Maximum distance travelled | $r^2 = 0.81$<br>$p < 0.001$ | $r^2 = 0.94$<br>$p < 0.001$ |
| Net square displacement | | $r^2 = 0.83$<br>$p < 0.001$ |

Furthermore, we calculated intra-individual repeatability of activity over time using the R package rptR (Stoffel et al. 2017, Version 0.9.22), which builds on linear mixed models fitted using lme4. We created three linear mixed models with a Gaussian error distribution, which included daily movement behaviour (maximum distance travelled, net squared displacement,

and diffusion rate, respectively) as the response variables, sex, and nights since tagging as fixed effects, and individual ID as a random effect. We calculated 95% confidence intervals by parametric bootstrapping (1000 iterations). We also tested the repeatability of activity separately for males and females, since repeatability in movement behaviour has been shown to differ between sexes in the eagle owl (*Bubo bubo*) (Campioni et al. 2013). To increase the normality of the model residuals all activity measures were log transformed prior to calculating repeatability.

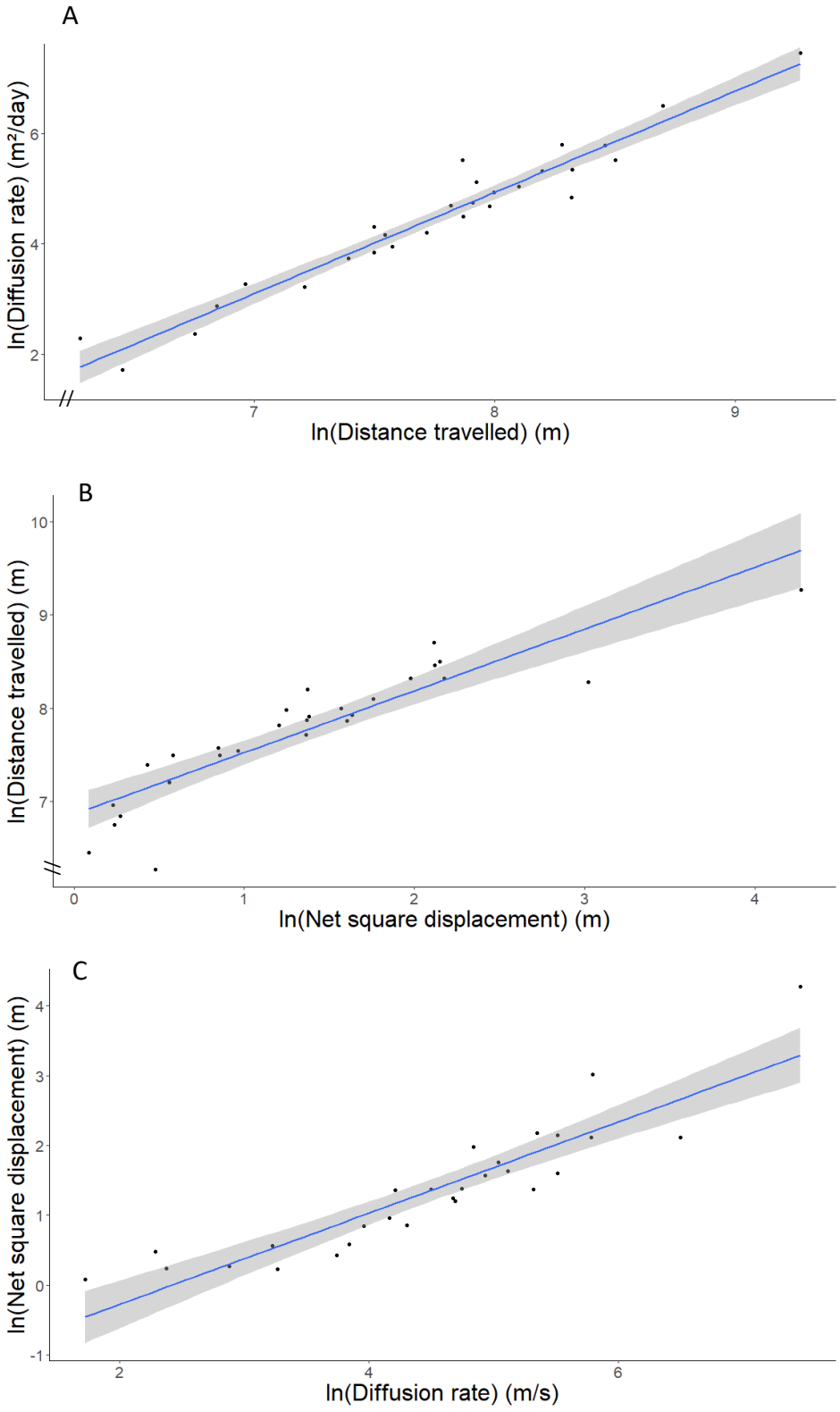


Figure 2: Scatterplots showing positive correlations between all three measures of activity (maximum distance travelled, net square displacement, diffusion rate) after ln transformation. A: $r^2 = 0.94$, $p < 0.001$, $n = 28$; B: $r^2 = 0.81$, $p < 0.001$, $n = 28$; C: $r^2 = 0.83$, $p < 0.001$, $n = 28$.

***Utilization distribution and personality***

We used Pearson's correlation tests to assess the association between our two boldness measures (number of struggles and FID) and all three activity measures (maximum distance travelled, net square displacement, and diffusion rate). We tested which factors predict utilization distribution using a linear model with ResBoldness, PC_Activity, sex, and the interaction between PC_Activity and sex as fixed effects. We chose to include this interaction because of the movement nature of our activity measures and different movement types have been shown to differ between sexes in owls (Catlin 2004, Becket and Proudfoot 2012, Séchaud et al. 2021, Campioni et al. 2013).

**Ethical note**

Permission to conduct this study was granted by the Galápagos National Park Directorate (DPNG) (PC-89-22). All owls were handled by or under supervision of two professional and experienced raptor banders (PS and SCS) to minimize stress and risk of injury. No owl suffered any obvious injury from being handled. The owls were released at their site of capture within 90 mins, and we found no obvious negative impact on the owl's health over the following nights.

## Results

**Boldness**

The mean ± SE number of struggles during handling was 27.4 ± 1.7 (range 12–47, n = 33) and mean ± SE flight initiation distance was 1.7 ± 0.23 m (range 0.55–5.00 m, n = 21). There was no difference between sexes in the number of struggles ($t(29) = -0.735$, $p = 0.469$) nor between sexes in FID ($t(17) = -1.079$, $p = 0.300$). Our cross-context comparison of boldness scores showed a statistically significant association: birds that struggled more during handling also had a shorter FID (Pearson $r^2 = 0.20$, $p = 0.040$, n = 21) (Fig. 3).

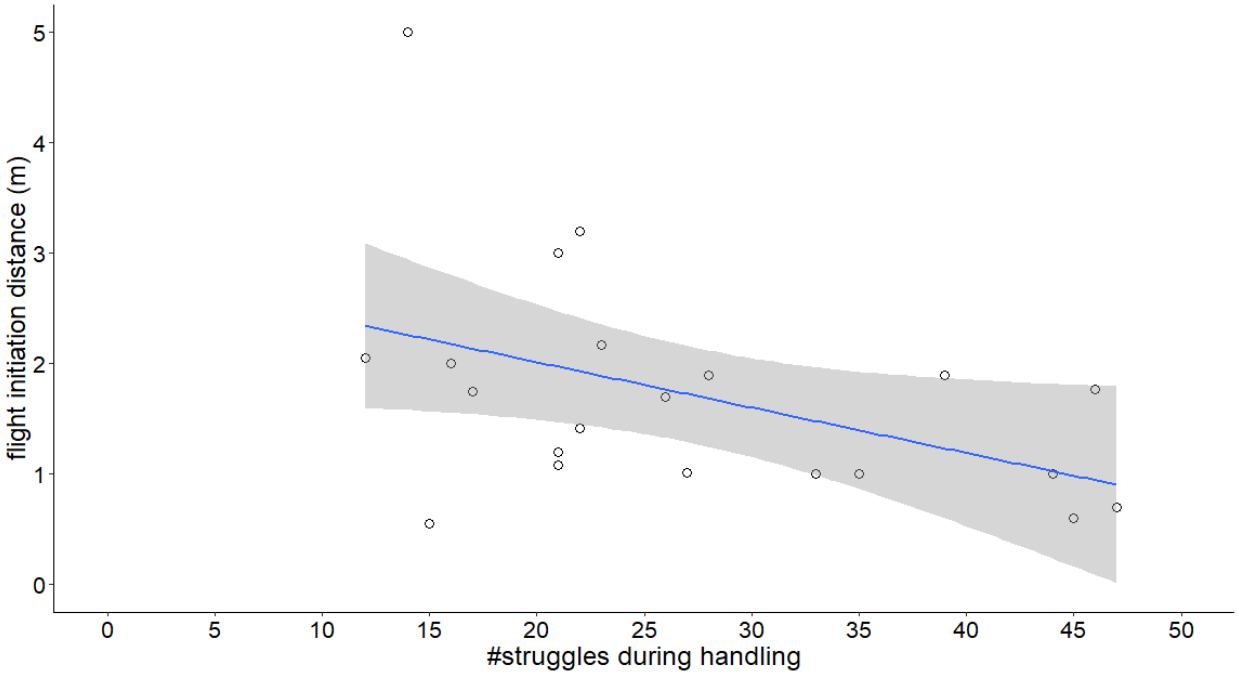


Figure 3: The significant association with 95% confidence intervals between two boldness measurements across contexts (total number of struggles during handling, flight initiation distance) in 21 Galápagos short-eared owls. Birds that struggled more when held by a human also had a shorter flight initiation distance when approached by a human (Pearson $r^2 = 0.20$, $p = 0.040$, $n = 21$).

**Activity**

We obtained activity data from 28 individuals (10 males and 18 females). The three measurements of activity were maximum distance travelled (mean ± SE = 2896 ± 386 m, range 530–10,628 m), diffusion rate (mean ± SE = 192 ± 62 m/s, range 5–1735 m/s) and net square displacement (mean ± SE = 6 ± 3 m, range 0.09–70 m).

The mean ± SE number of nights tracked per owl was 25 ± 3.2 (range 3–58). Activity measurements per individual were highly repeatable over time ($R > 0.4$, $p < 0.001$, Table 3). The repeatability of the activity measurements did not differ between sexes (Table 3). Females had higher PC_Activity scores than males ($t(26) = 2.147$, $p = 0.041$), which would indicate a higher activity level.

Table 3: Overall repeatability of the three activity measurements (maximum distance travelled, net square displacement and diffusion rate) and separated by sex. The whole population was significantly repeatable, and both sexes were repeatable as well when tested separately.

| | Maximum distance travelled | Net square displacement | Diffusion rate |
|---|---|---|---|
| Males | R = 0.322<br>SE = 0.113<br>CI = 0.086 - 0.517<br>p < 0.001 | R = 0.318<br>SE = 0.106<br>CI = 0.111 - 0.515<br>p < 0.001 | R = 0.326<br>SE = 0.111<br>CI = 0.096 - 0.526<br>P < 0.001 |
| Females | R = 0.403<br>SE = 0.097<br>CI = 0.193 - 0.577<br>p < 0.001 | R = 0.381<br>SE = 0.096<br>CI = 0.187 - 0.551<br>p < 0.001 | R = 0.376<br>SE = 0.094<br>CI = 0.173 - 0.534<br>p < 0.001 |
| Combined sexes | R = 0.419<br>SE = 0.077<br>CI = 0.266 - 0.562<br>p < 0.001 | R = 0.392<br>SE = 0.072<br>CI = 0.237 - 0.517<br>p < 0.001 | R = 0.403<br>SE = 0.072<br>CI = 0.252 – 0.530<br>p < 0.001 |

**Utilization distribution**

We collected a total 17 863 GPS fixes from 30 individuals (10 males and 20 females; average = 576 fixes per owl; min = 59; max = 1095). But two owls were removed from analysis because they didn't fulfill the requirements to calculate AKDEs. Excluding these two individuals owls were tracked on average for 25 ± 3.14 nights (range= 3–58). The mean ± SE utilization distribution was 33.93 ± 6.14 km² (range 2.46–104.66 km²). Females (55.96 ± 12.75 km²) had larger utilization distributions than males (12.84 ± 5.04 km²) (Welch-Test: t(20.9)=2.989, p = 0.007) (Fig. 4).

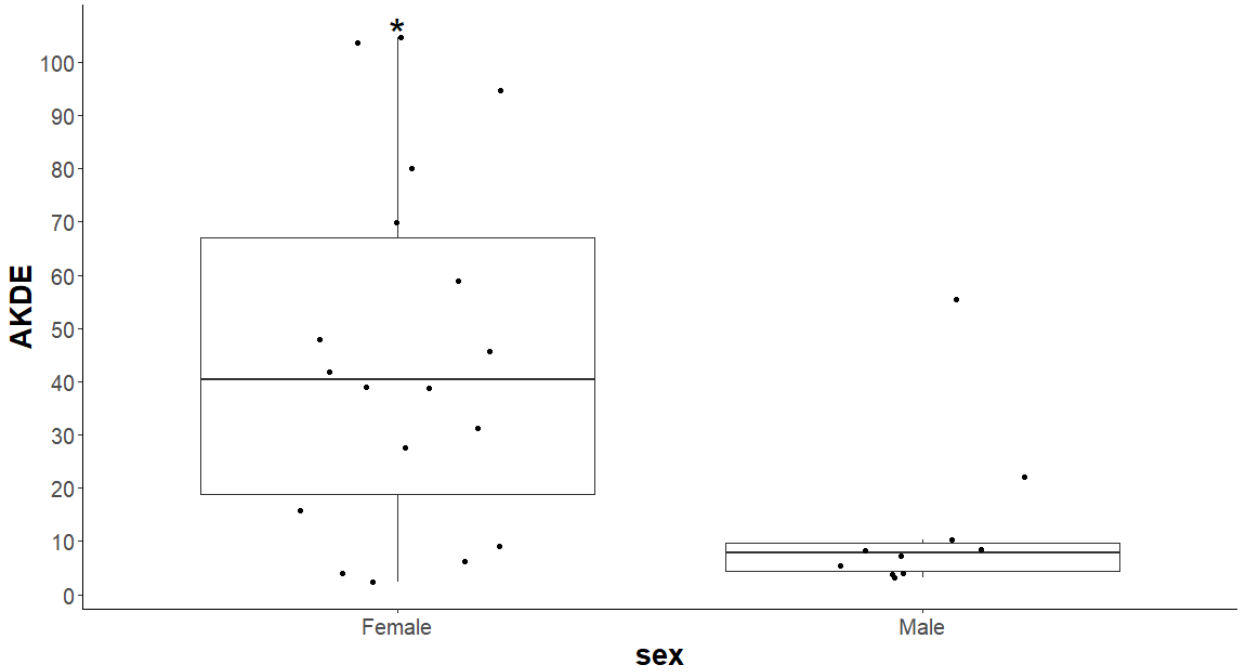


Figure 4: Boxplot showing utilization distribution size (AKDE) in female and male Galápagos short-eared owls. Females (mean = 55.96, SE = 12.75, n = 18) had larger utilization distributions than males (mean=12.84, SE=5.04, n=10). Welch-Test: t = 3.4917, df = 25.6, p = 0.002. Utilization distribution was estimated with autocorrelated kernel density estimation (AKDE).

**Utilization distribution, activity and personality**

The linear model revealed no significant result (Table 4).

Table 4: Output from a linear model testing which factors predict utilization distribution in Galápagos short-eared owls. The model included ResBoldness (residuals of ANOVA between both boldness measures), PC_Activity (principal component combining three activity measures), sex (male, female), and the interaction between activity and sex as fixed effects. Significant results are marked in bold.

| Fixed effects | Estimate | SE | t | p |
|---|---|---|---|---|
| Intercept | 44.38765 | 11.73767 | 3.782 | **0.003** |
| ResBoldness | 0.06057 | 0.85701 | 0.071 | 0.945 |
| PC_Activity | 8.58126 | 5.45686 | 1.573 | 0.144 |
| Sex | -43.90491 | 21.80000 | -2.014 | 0.069 |
| Activity:Sex | -21.35957 | 13.93340 | - 1.533 | 0.154 |

## Discussion

Research on personality in owls is sparse and currently limited to only a few species (Luna et al. 2020, Da Silva et al. 2013, Carrete and Tella 2010, van den Brink et al. 2012a). Here, we used both observational (GPS data) and experimental (struggles during handling, flight initiation distance) approaches to quantify personality in the Galápagos short-eared owl. Our study is the first to investigate personality in this species and one of the few to measure personality traits across contexts in an owl species (see also Carrete et al. 2017, Cavalli et al. 2016). It is also the first to have tested the association between personality and utilization distribution in any owl species. As we predicted, our two measures of boldness were significantly correlated, with owls that struggled more during handling also fleeing from an approaching human at shorter distances. Similarly, all three measurements of activity (maximum distance travelled, net square displacement, and diffusion rate) strongly correlated with one another and were highly repeatable over time. We found no effect of personality on utilization distribution, but females had significantly larger utilization distributions.

Our two measures of boldness, number of struggles and FID, were significantly negatively correlated. Meaning that individuals that struggled more when being held also flew off at a shorter distance when a human was approaching. Our results indicate that FID and handling response might be underpinned by the same personality trait (boldness) in Galápagos short-eared owls. In Yellow-spotted Monitors (*Varanus panoptes*) a similar relationship as in our study between struggles while being handled and FID was found (Ward-Fear et al. 2018), but no such association was found in yellow-bellied marmots (*Marmota flaviventris*) (Petelle et al. 2013). In owls these two boldness assays have never been tested against each other, but in burrowing owls rural owls showed a correlation between FID from an approaching human and latency to approach a perceived natural predator (Carrete and Tella 2017) as well as from an approaching human with a dog (Cavalli et al. 2016). We acknowledge that we do not have

repeatability for either variable, which was not possible as the owls could not be resighted more than once or twice, or recaught, despite our efforts to do so. However, repeatability for both variables has been shown in other owl species (Carrete and Tella 2010, Carrete and Tella 2013, van den Brink et al. 2012a). This study tests for an association between handling response and FID, and finds the expected correlation, supporting the cross-context validation of these two variables as measures of the boldness personality axis (for detailed discussion see Ploderer 2024, chapter 2).

Activity is most often measured experimentally using an open-field test (reptiles: Cromie and Chappel 2012; mammals: Wirth-Dzieciolowska et al. 2005, Montiglio et al. 2010; amphibians: Maes et al. 2013, Hammond et al. 2020; birds: Colombelli-Négrel et al. 2022). However, these assays often include an element of novelty, despite recommendations by Réale et al. (2007) that activity be measured in a non-novel and non-risky environment. Use of GPS data to quantify an individual's landscape-level movements provides a measure of activity from wild, free-roaming individuals behaving in a natural context. Here, we showed that GPS data can provide a consistent measure of activity at the landscape levels, with all three activity variables highly correlated and repeatable across time. A previous study with brown bears (*Ursus arctos*) also quantified personality measurements (boldness, activity, and exploration) solely from GPS movement data (Hertel et al. 2019). This allows for a much more natural way of measuring personality. The development of increasingly precise GPS tracking technologies, which could even incorporate accelerometer data, opens an array of possibilities for measuring activity in vivo. Overall dynamic body acceleration (ODBA) has been originally developed as a proxy for energy expenditure in vivo using acceleration data (Wilson et al. 2006, Gleiss et al. 2011) and can be a powerful tool to measure activity in a

natural context (Stiegler et al. 2022). This technique requires data with high resolution and could not be applied in this study because our loggers only collected activity reports.

Female owls were more active than males and both sexes were repeatable. Sex-dependent differences in personality traits and their repeatability are a known phenomenon (Nakagawa et al. 2007, Debeffe et al. 2015, Thomson et al. 2020). In many studies, males have been reported to show higher levels of repeatability (Nakagawa et al. 2007, Jenkins 2011, Schwagmeyer and Mock 2003), although a review by Bell (2009) covering an array of taxa found no indication that one sex was more repeatable than the other. Similarly, a recent meta-analysis by Harrison et al. (2022) found no support for the "greater male variability hypothesis" (but see del Giudice and Gangestad 2023). In a study of eagle owls (*Bubo bubo*), movement behaviour was more repeatable in males, which was explained by the higher territoriality of the males (Campioni et al. 2013). Future research into the biology of the Galápagos short-eared owl, and particularly the division of duties between males and females, may reveal an ecological explanation for the differences in landscape movement observed in this study.

We found that females had significantly larger utilization distribution than males. Across owl species, home range differences between sexes varied according to reproduction cycle (Henrioux 2000, Sunde et al. 2003) and habitat (Redpath 1995, Sunde and Redpath 2006, Lövy and Riegert 2013). Our results better fit the sex-dependent differences found in barn owls (*Tyto alba*) (Séchaud et al. 2021, but see Cain et al. 2023) and eagle owls (*Bubo bubo*) (Campioni et al. 2013). In both studies, males had a smaller home range than females. While the larger home ranges of males in tawny owls (*Strix aluco*) and long-eared owls (*Asio otus*) have been explained by the males taking over most of the hunting during reproductive

periods (Henrioux 2000, Sunde et al. 2003), high population density, high territoriality and high male-directed aggression were seen as the reason why barn owl and eagle owl males had smaller home ranges (Séchaud et al. 2021, Campioni et al. 2013). In barn owls, female extra-pair bonding may contribute to larger home ranges: males are restricted to their territory and cannot leave because they risked being attacked by their neighbours, whereas females are allowed to roam free (Séchaud et al., 2021). To date, too little is known about the biology of the Galápagos short-eared owl to understand the mechanisms driving these sex differences in home range. No detailed study on their reproductive cycle has been conducted, although active nest sites have been found nearly year-round: one was found in December, and another recently abandoned one in April (De Groot 1982). Another one was reported in May (Lack 1949), and we found one active nest in February 2022 and several others from July to September 2023 (personal observations). This nearly year-round breeding cycle contrasts with that of the nominate form in Europe and North America, which typically lasts from March to June (Wiggings 2020). More basic research on the subspecies' biology is needed to provide additional context on the movement patterns identified in this study.

Contrary to our expectations, we found no link between an owl's personality traits (boldness, activity) and the size of its utilization distribution. Home range size is influenced by personality in a diverse range of animal species, including common brushtail possums (*Trichosurus vulpecula*) (Wat et al. 2020), monitor lizards (*Varanus panoptes*) (Ward-Fear et al. 2018), and European hares (*Lepus europeaus*) (Stiegler et al. 2022). In short-eared owls, individuals' movement ecology may be more strongly driven by non-behavioural factors, such as sex. In burrowing owls and barn owls, bolder individuals had greater natal and/or breeding dispersal distances than their counterparts (Luna et al. 2019. Luna et al. 2020, van den Brink et al. 2012b). However, these findings are not necessarily comparable to ours, as

dispersing individuals do not have a home range per definition (Burt 1943). It is also possible that home range is influenced by personality traits that we did not measure, such as exploration (Spiegel et al. 2017). More research into personality and its effects on home range in owls is needed to answer that question.

Our study is the first to examine the possible relationship between personality and home range size in the short-eared owl. We used fear response towards humans as measure of boldness and extracted three movement activity parameters from GPS data as measure of activity. We found no correlation between either of the two personality axes and the size of the utilization distribution of the owls. Nevertheless, these results can help us understanding the effects personality has on movement behaviour. Future studies should measure a wider range of behavioural traits, including exploration, and validate their temporal consistency.

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**Image References**

Figure 1, a) Sumasgutner, C. S. (2023), taken on Floreana island, Galapagos during Data collection

Figure 1, b) Arteaga-Torres, J. (2023), taken on Floreana island, Galapagos during Data collection

Figure 1, c) Ploderer, J. (2023), taken on Floreana island, Galapagos during Data collection

## Supplementary Material

### Harnessing guide for Galápagos short-eared owls

For the leg-loop harness, two 40 cm Teflon straps were first threaded through a 6.5 mm aluminium clamp (Ecotone) and then through the front loop of the loggers and back through the aluminium clamp. The clamps where then closed using electricity pliers. The two loose ends were threaded through an aluminium clamp, and either the left or right back loop of the logger in the same manner, except that the clamps were not sealed this time. To fit the logger onto an owl, each leg was placed through one of the Teflon loops and the logger positioned on the pelvis, with the three antennae pointing backwards. The Teflon loops were then tightened to the same length, so that the logger was not sitting tight onto the bird but also not moving much.

Once in position, the two aluminium clamps were sealed, and the remaining Teflon straps cut off. The backpack harness had two shorter straps (140 mm long) and two longer Teflon straps (200 mm long) made from Teflon. Additionally, a 24 × 24 mm square of kangaroo leather with an 8 × 8 mm square hole was used as the centrepiece of the harness. One end of the Teflon straps was put through the inside leather ring, flapped back over the leather, and sewn together using dental floss. A drop of superglue was placed inside the Teflon tube to prevent the Teflon threads from unthreading. This was repeated with all four straps. The straps could still slide along the leather rim. The two shorter straps were placed next to each other in front and the longer straps at the back. The two front straps were threaded through one aluminium clamp each, then through the two front loops of the loggers, and then back through the clamps. Next, the back straps were threaded through the aluminium clamps and left loose until the harness was fitted to an owl.

To fit the logger, the owl's head was placed through the front part of the harness, so that the logger sat on the back of the owl and the antennae was facing backwards. The leather loop was positioned on top of the sternum keel. The back straps were brought back, crossing the scapula, and threaded through the back loops of the loggers, and then back through the aluminium clamp. Before sealing the clamps, all straps were adjusted so that both front straps and both back straps were the same length. All straps were placed so that they were as close to the owl's skin as possible, without any feathers caught between the straps and the body. The final position of the logger was on the middle/lower back, in such a way that the solar panels were not covered by feathers. Once in place, all surplus straps of Teflon were cut off.