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Response of flower-visiting hummingbirds to sit-and-wait predators: Effects of foraging behaviour and body size

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Abstract

Predation risk is a key factor influencing the foraging behaviour of pollinators. Hummingbirds (Trochilidae), as frequent flower visitors, are potential targets of sit-and-wait predators such as snakes and praying mantises. This study experimentally examined how differences in body size and subfamily (hermits versus true hummingbirds) influence the behavioural responses of flower-visiting hummingbirds when exposed to predators. Using video analyses from 840 hours of observations conducted in La Gamba, Costa Rica, the reactions of eleven hummingbird species were compared across three treatments: snake dummies, mantis dummies, and a neutral control (white napkins). Behavioural parameters such as predator-approaching duration and flower visit duration were quantified and analysed using Generalised Linear Mixed Models (GLMMs).

Results revealed that treatment type significantly affected hummingbird behaviour. Overall, hummingbirds spent nearly twice as long approaching predator dummies as compared to the control. No significant differences were found between subfamilies. Larger species tended to display longer visit durations in the presence of predators, suggesting either reduced fear or increased territorial boldness. These findings indicate that body size influences anti-predator behaviour in hummingbirds, while foraging strategy (territorial versus trap-lining) appears less important.

Keywords

predator avoidance, anit-predatory behaviour, predator approaching time, foraging behaviour, body size, sit-and-wait predators, hermits, true hummingbirds

Zusammenfassung

Das Prädationsrisiko ist ein entscheidender Faktor, der das Nahrungssuchverhalten von Bestäubern beeinflusst. Kolibris (Trochilidae) sind als häufige Blütenbesucher potenzielle Ziele von Lauerjägern wie Schlangen und Gottesanbeterinnen. In dieser Studie wurde experimentell untersucht, wie Körpergröße und Zugehörigkeit zu unterschiedlichen Unterfamilien (hermits versus true hummingbirds) die Verhaltensreaktionen blütenbesuchender Kolibris bei der Konfrontation mit Prädatoren beeinflussen. Anhand von Videoanalysen aus insgesamt 840 Beobachtungsstunden in La Gamba, Costa Rica, wurden die Reaktionen von elf Kolibriarten in drei Behandlungsgruppen verglichen: Schlangen-Attrappen, Gottesanbeterinnen-Attrappen und eine Kontrollgruppe (weißes Taschentuch). Verhaltensparameter wie die Dauer der Annäherung an den Prädator sowie die Blütenbesuchsdauer wurden quantifiziert und mithilfe Generalisierter Linearer Gemischter Modelle (GLMMs) ausgewertet.

Die Ergebnisse zeigten, dass die Art der Behandlung einen signifikanten Einfluss auf das Verhalten der Kolibris hatte. Insgesamt benötigten die Vögel nahezu doppelt so lange, um sich den Prädator-Attrappen zu nähern, verglichen mit der Kontrollbedingung. Zwischen den Unterfamilien traten keine signifikanten Unterschiede auf. Größere Arten zeigten tendenziell längere Besuchsdauern in Anwesenheit potenzieller Prädatoren, was entweder auf eine geringere Scheu oder auf ausgeprägtere territoriale Kühnheit hindeuten könnte. Die Befunde legen nahe, dass die Körpergröße das Antiprädatorverhalten von Kolibris beeinflusst, während die Nahrungssuchstrategie (territoriales Verteidigen versus Trap-lining) eine geringere Rolle spielt.

Acknowledgements

I would like to thank my supervisor, Dipl.-Biol. Dr. Christian H. Schulze, for giving me the opportunity to conduct my research on hummingbirds in Costa Rica and for his guidance throughout the preparation of this master's thesis. My thanks also go to the Tropical Field Station La Gamba for providing the necessary research facilities, equipment, accommodation, and kind assistance during my stay. Special thanks are due to Markus Bauriedl for his help with video data storage and technical support during my stay at the Field Station. I am furthermore grateful to the University of Vienna for awarding me the scholarship that made this research possible. Finally, I wish to thank my life partner, Mathias Zach, for his continuous encouragement, patience, and unwavering support throughout this project and beyond.

Contents

1 Introduction

The hummingbirds (family Trochilidae) represent one of the largest avian families with about 335 species (West & Butler, 2010). Since they feed on flower nectar, hummingbirds act as important pollinators for many plants. Due to their frequent visits of flowers to exploit nectar, they are potentially attractive prey for sit-and-wait predators. Such predators remain mostly stationary and, therefore, depend on sites where prey passes frequently, e.g. flowering plants that are visited by pollinators (Higginson *et al.*, 2009). However, since predation events occur not frequently enough for collecting data on the predation risk in the field through observations of flower-visiting hummingbirds, we tested experimentally to what extent hummingbirds are capable to recognize potentially dangerous sit-and-wait predators at flower sources. Potential sit-and-wait predators which may represent a risk for hummingbirds could be snakes, lizards and even praying mantises (Fogden & Fogden, 2006; Lorenz, 2007; Nyffeler *et al.*, 2017).

However, the results of species' risk assessment and their behavioural response to sit-and-wait predators may be species-specific, depending on body size and foraging behaviour. While praying mantises and other small predators can pose a threat to smaller species, they are probably relatively harmless to larger species. The body size of hummingbirds varies strongly, ranging from a body length as small as 5 cm and a body mass of 1.6 grams in species like *Phaethornis ruber* and *Mellisuga helenae* to 22 cm and 21 grams in *Patagona gigas* (Schuchmann, 1999; West & Butler, 2010). Related to the hummingbirds in the region La Gamba the smallest species by body length is the *Lophornis adorabilis* as small as 6.5 cm and the tallest is *Phaethornis longirostris* with up to 17 cm. But especially in hummingbirds, long tail feathers are common, which is why size is primarily defined by weight rather than body length. For instance, *Phaethornis longirostris* measures 17 cm in length but weighs only 6.4 grams, whereas *Phaeochroa cuvierii* reaches just 12.5 cm in length yet weighs 8.98 grams (Schuchmann, 1999; Dyer & Howell, 2023; Riedl & Schulze, 2010).

Based on their foraging habits, two different behaviours can be observed between the two subfamilies, the true hummingbirds (trochilines) and the hermits. According to West and Butler (2010), true hummingbirds tend to exhibit territorial behaviour to protect their food sources against conspecifics or other nectarivores birds. Therefore, it is likely that predators are also attacked by males to protect their food sources, which are linked to their mating opportunities. In contrast, male hermits gather in groups called leks to attract females and thus do not show any territorial behaviour (West & Butler, 2010). These lek species are specialized "trapliners"; they visit undefended isolated flowers containing large amounts of nectar (Gill, 1988; Thiel *et al*., 2021). In the region La Gamba four hermit species can be found (*Glaucis aenea, Threnetes ruckeri, Phaethornis longirostris* and *Phaethornis striigularis*) (Tebb, 2008; Riedl & Schulze, 2010).

In this study, dummies of snakes and praying mantises were exposed to hummingbirds near to visited flowers to simulate predation risk. Using this experimental approach, the following research questions were addressed:

(1) Do smaller hummingbird species perceive praying mantises as higher risk than larger hummingbirds, while the risk assessment when exposed to snakes does not differ between species?

(2) Do trap-lining species (hermits) attack predators less intensively than territorial species (true hummingbirds) since flowering plants represent an important requisite of their territories and, hence, maintaining access to these local nectar sources is particularly important for true hummingbirds?

2 Material and methods

2.1 Study area

The research was conducted in November 2024 at the La Gamba Field Station (N 8°42.61', W 83°12.97'; elevation: 70 m above sea level) and surrounding areas. Additionally, the study included research on higher-lying property of the Field Station, known as Finca Alexis (N 8°45'44.492'', W 83°9'58.424''; elevation 359 m above sea level). GPS coordinates for the video locations can be accessed through the following link:

https://www.google.com/maps/d/edit?mid=1C2_ku0KNhCki_hwV8XZcfzVAci2Ln3s&usp=sharing.

The research videos were taken between October 31st and November 24th 2024. To maximise the sample, data from previous research was used. Specifically, this included data collected by Neuhold between March 15th and June 1st 2017 as well as observations collected by two student groups from July 28th to August 9th 2014 and November 12th to 23rd 2015 (Neuhold, 2018). All observations collected identical variables. While most of the data from the student groups was based on real-time observations, Philipp Neuhold relied exclusively on video analysis.

2.2 Field experiments

To increase the likelihood of successful recordings, only flowering plants that were frequently visited by hummingbirds were selected. The corresponding location data (plant species, weather and location description) and the GPS data were determined. When positioning the camera, attention was paid to the distance between the camera and the flowers to ensure that the hummingbirds were not disturbed by the cameras. Depending on the structure of the selected plant the camera had at least a distance of 40 cm to the flower. In addition, the cameras were positioned at a minimum distance of 20 metres from each other to increase the likelihood of different individuals. Some areas were re-filmed after a few days, especially if a different species was discovered at the location or if the previous footage was not very informative (e.g. no hummingbird visits). To withstand the wet weather conditions action cams of the brand GoPro (GoPro Hero, GoPro 3, GoPro 7) were used. The observation was divided into two periods. In the first hour hummingbird visits were filmed without any manipulation of the plant. Then, in the second hour flower visits were documented either with two white napkins fixed in the plant (to test how hummingbirds respond to a “new unfamiliar object”) (treatment 1), with two dummy praying mantises fixed on or near flowers (treatment 2) or with two dummy snakes fixed on or near flowers (treatment 3). The praying mantises were green and brown and 11 cm long (Fig. 1). The snakes were green with a yellow belly and about 58 cm long (Fig. 2).

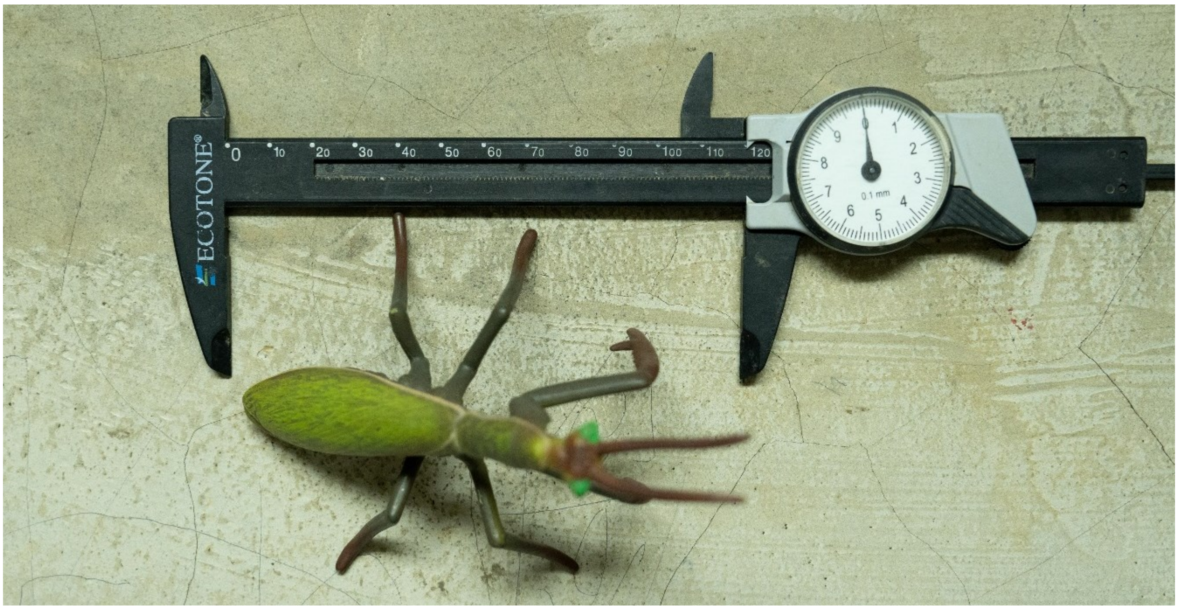


Fig. 1 Dummy of mantis

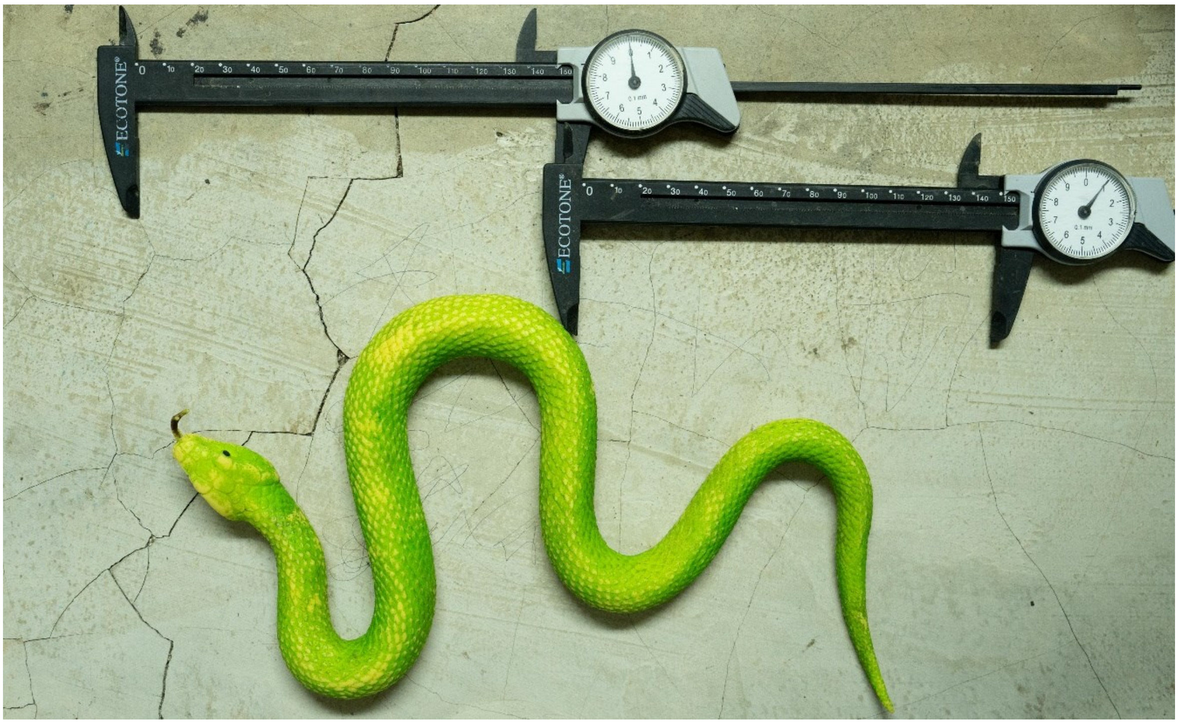


Fig. 2 Dummy of snake

To analyse the behavioural response of hummingbirds to the dummy predators, the time spent approaching the napkins and the two different dummy predators was quantified.

A total of 82 videos were recorded over one month of observation. Of these, 62 videos were successful, which means at least one hummingbird visited the flowers during filming. In 20 cases there was no hummingbird visit in the first and second hour. In 28 videos there was no flower visit in the second hour of observation. In total, 357 experiments could be analysed including the data of the previous studies. Of these, 273 were successful and 254 showed a flower visit in the second hour.

2.3 Plant and hummingbird species

During the most recent observation period in November 2024, a total of 24 distinct plant species visited by hummingbirds were recorded. Combined with data from the previous studies, this brings the total to 36 plant species, encompassing 249 individual plants. Some of these plants were filmed multiple times with at least five days between each observation to avoid a learning effect.

This study documented the following 36 plant species visited by hummingbirds: *Calathea crotalifera, Calathea lutea, Calathea marantifolia, Calathea platystachya, Cheilocostus speciosus, Columnea polyantha, Costus pulverulentus, Costus speciosus, Costus stenophyllus, Drymonia macrophylla, Erythrina costaricensis, Etlingera elatior, Guzmania scherzeriana, Heliconia collinsiana, Heliconia danielsiana, Heliconia imbricata, Heliconia latispatha, Heliconia psittacorum, Heliconia rostrata, Heliconia* sp., *Heliconia stricta, Heliconia wagneriana, Hibiscus rosa-sinensis, Kohleria allenii, Malvaviscus arboreus, Marantochloa purpurea, Palicourea* sp., *Pentagonia tinajita, Petrea volubilis, Psychotria elata, Psychotria poeppigiana, Sanchezia speciosa, Stachytarpheta frantzii, Stachytarpheta jamaicensis, Thunbergia grandiflora* and *Werauhia gladioliflora.*

Previous studies have documented the presence of 20 hummingbird species in the region La Gamba (Tebb, 2008; Riedl & Schulze, 2010). A total of 11 different species were filmed during the observation periods so far. During the most recent observation period in November 2024, 10 hummingbird species were recorded on film. The recorded hummingbirds were identified according to Dyer & Howell (2023) and

Garrigues & Dean (2014). Of these species, 9 were observed during the first and second hour and could therefore be included in the analysis: *Amazilia tzacatl* (n = 52), *Glaucis aeneus* (n = 16), *Klais guimeti* (n = 9), *Phaeochroa cuvierii* (n = 12), *Phaethornis longirostris* (n = 35), *Phaethornis striigularis* (n = 62), *Poyerata decora* (n = 14), *Thalurania colombica* (n = 9), and *Threnetes ruckeri* (n = 45). The species *Chlorestes eliciae* (Neuhold, 2018) and *Heliomaster longirostris* were only recorded in the first hour of filming. Therefore, no reaction to the treatments could be documented, leading to an exclusion in the analysis.

To answer the research question, it was necessary to sort the species by size and subfamilies. The family Trochilidae is divided into hermits (*Glaucis aeneus, Phaethornis longirostris, Phaethornis striigularis, Threnetes ruckeri)* and true hummingbirds (*Amazilia tzacatl, Klais guimeti, Phaeochroa cuvierii, Poyerata decora, Thalurania colombica, Chlorestes eliciae*, *Heliomaster longirostris).* Body size of the species was quantified as mean body mass of individuals mist netted at La Gamba in recent years (Tab. 1).

Tab. 1 Mean body mass of hummingbirds species based on the body weight measurements of individuals mist-netted at La Gamba, Costa Rica during the last years (N = number of weighed individuals). Species are sorted according to increasing body mass.

hummingbird species	**N**	**mean body mass (g)**	**± standard deviation**
Phaethornis striigularis	79	2.59	0.50
Klais guimeti	22	3.55	0.41
Chlorestes eliciae	5	3.90	0.52
Thalurania colombica	113	4.24	0.31
Poyerata decora	58	4.44	0.23
Amazilia tzacatl	90	4.96	0.38
Glaucis aeneus	14	5.27	0.45
Phaethornis longirostris	186	6.15	0.49
Threnetes ruckeri	298	6.21	0.44
Heliomaster longirostris	1	6.40	
Phaeochroa cuvierii	13	8.98	0.98

2.4 Video analysis

During the most recent observation period in 2024, a total of 162 hours of video material were collected. For the statistical analysis, data from previous observation periods in 2017, 2015, and 2014 were also incorporated. The 2017 observation period yielded 496 hours of video material, while the student groups from 2014 and 2015 contributed 42 hours of video recordings and 140 hours of real-time observations. Altogether, this amounts to a total of 840 hours of observation.

The video material was analysed using VLC Media Player, with playback speed initially set to 3x for efficient viewing. Upon detecting a hummingbird visiting the flowers, the playback was paused and subsequently slowed to 0.25x speed to accurately record the following parameters, which were essential for the data analysis: the hummingbird species, the time and duration of the plant visit, the number of visited flowers and the predator approaching duration. If the hummingbird was out of the video frame for more than five seconds before returning to the plant, this was recorded as a new approach.

2.5 Data analysis

The statistical analyses were conducted using the software SPSS. Data from all four observation periods (2014, 2015, 2017, and 2024) were included. However, experiments that did not record any visits during the second observation period were excluded from the analysis.

Initially, a one-way ANOVA was planned. As the ANOVA did not yield sufficiently informative results, a Generalized Linear Mixed Model (GLMM) was additionally applied. The experiments without predator approaching (predator approaching time = 0 seconds) were removed for the GLMM because SPSS does not include zero values in the analysis. This may be considered critical, as the lack of response to predators is also a result. Therefore, the zero-values were analysed separately. Since the values do not follow a normal distribution, a histogram was created. This showed many low values and some very high values that were rare. After further comparison of the mean with the variance (showing a large difference), a Negative Binomial distribution was assumed. However, since some of the second values are given as decimal numbers and a negative binomial regression can only read whole numbers, a Gamma distribution was used as the target distribution for the GLMM. In summary, a GLMM with Gamma distribution and a log-link function was conducted.

To determine whether the hummingbirds' reactions to the predators (snakes and mantises) significantly differed from the control group (napkins) bird species, treatment and their interaction were chosen as fixed effects. No random variables were specified, as this always led to error warnings. For the treatment-specific analyses the fixed variable was bird species. The species *Klais guimeti* had to be removed in some cases due to low statistical relevance (one single case) e.g. duration approaching predators. For the mean visit duration of the second observation hour grouped in snakes, mantises and napkins the treatment was used as fixed and the species as random variable.

However, the residual variance parameter (i.e., the error that the model could not explain) in the GLMM was significant. This means the model had a non-negligible amount of unexplained variability in the data. The consistently very low p-value (< 0.001) and the high Z-value confirm that this result is highly significant. Overall, this means that in the models performed, there is a significant amount of unexplained error that has not yet been accounted for by the fixed effects (species, treatments and their interaction effect). The high error susceptibility of the model estimates suggests that the effect estimates are highly uncertain. This could be due to the high variability within the data. Therefore, the results should be interpreted with caution.

To illustrate the mean presence of hummingbird species during the second hour of filming, a bar chart was used, providing a clear and easily readable representation of the mean values. For comparing the mean values between the first and second hour across treatments, a plot including means and confidence intervals was employed to visualise the uncertainty resulting from the small sample size.

3 Results

3.1 Sample size

A total of 254 flower visits by different hummingbirds were analysed. It was assumed that repeated visits by the same species within one filming hour were made by the same individual. According to this definition, flower visits were observed from 85 individuals at the treatment snake, 94 individuals at the treatment mantis, and 75 individuals at the treatment napkin (Tab. 2).

Tab. 2 Sample sizes sorted by treatment and hummingbird species according to their weight (lightest species = first, heaviest species = last).

hummingbird species	N snake	N mantis	N napkin
Phaethornis striigularis	19	24	19
Klais guimeti	1	3	5
Thalurania colombica	3	6	0
Poyerata decora	3	5	6
Amazilia tzacatl	15	19	18
Glaucis aeneus	9	5	2
Phaethornis longirostris	11	13	11
Threnetes ruckeri	21	12	12
Phaeochroa cuvierii	3	7	2

3.2 Reaction on treatments

The GLMM revealed a significant effect for the fixed variable "bird species" ($p = 0.009$), indicating that different species respond differently to the predators. Additionally, the fixed variable "treatment" showed a significant effect ($p < 0.001$), suggesting that the type of treatment influences the predator approaching time. Also a significant interaction between “treatment” and “species” was observed ($p = 0.001$), indicating that the effect of the treatment varied among species. Predator approaching time was almost twice as long when hummingbirds were exposed to snakes and praying mantises compared to napkins (Fig. 3).

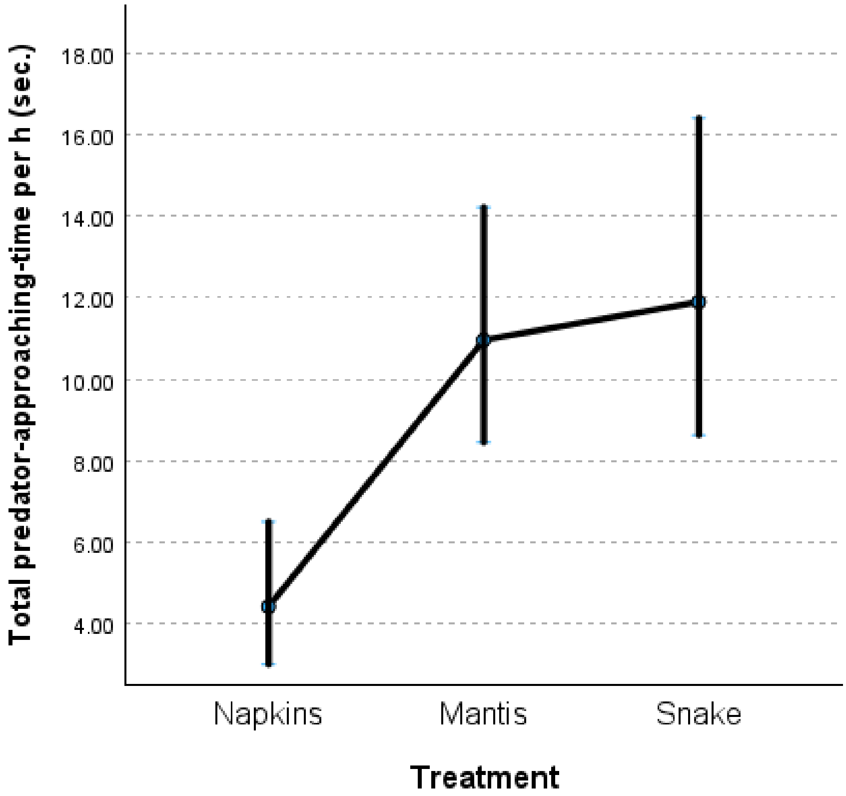


Fig. 3 Mean total duration (seconds per hour) (± 95% CI) spent approaching different types of predators (napkins, mantis and snake).

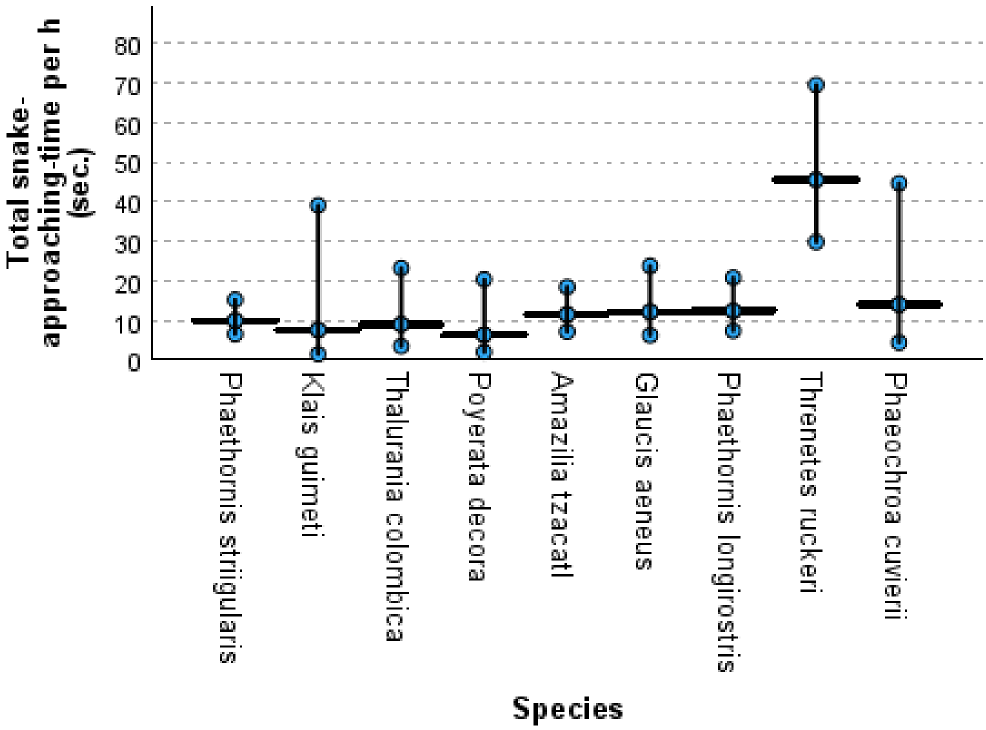
3.3 Duration approaching predators

The analysis of the total duration spent approaching the predator per hour in seconds yielded different results for the three treatments. In the snake treatment, the GLMM showed a significant effect of the fixed variable "bird species", indicating that different species respond differently to snakes. In particular, *Threnetes ruckeri* differed significantly from the other species – except for *Phaeochroa cuvierii* – and exhibited by far the highest predator approaching time per hour (Fig. 4a).

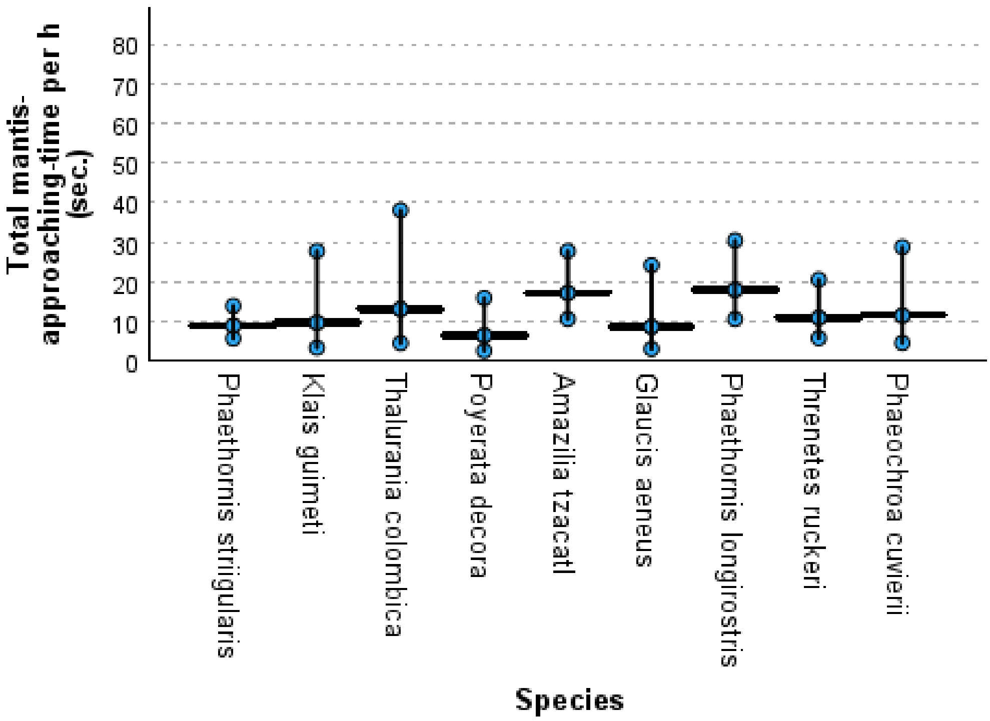
For the mantis treatment, the analysis did not reveal a significant effect ($p = 0.345$), indicating that the species did not differ significantly in their total reaction time per hour. Similarly, no significant differences were found between individual species and the reference group *Threnetes ruckeri* (Fig. 4b)

In the napkins group, however, a significant effect of the fixed variable "bird species" was detected ($p = 0.038$), indicating that the species differ in their napkin approaching time per hour. A significant difference was particularly found between *Threnetes ruckeri* and *Klais guimeti* ($p = 0.018$) (Fig. 4c).

(a)


Total snake-approaching-time per h (sec.)
80
70
60
50
40
30
20
10
0
Phaethornis striigularis
Klais guimeti
Thalurania colombica
Poyerata decora
Amazilia tzacatl
Glaucis aeneus
Phaethornis longirostris
Threnetes ruckeri
Phaeochroa cuvierii
Species

(b)


Total mantis-approaching-time per h (sec.)
80
70
60
50
40
30
20
10
0
Phaethornis striigularis
Klais guimeti
Thalurania colombica
Poyerata decora
Amazilia tzacatl
Glaucis aeneus
Phaethornis longirostris
Threnetes ruckeri
Phaeochroa cuvierii
Species

(c)

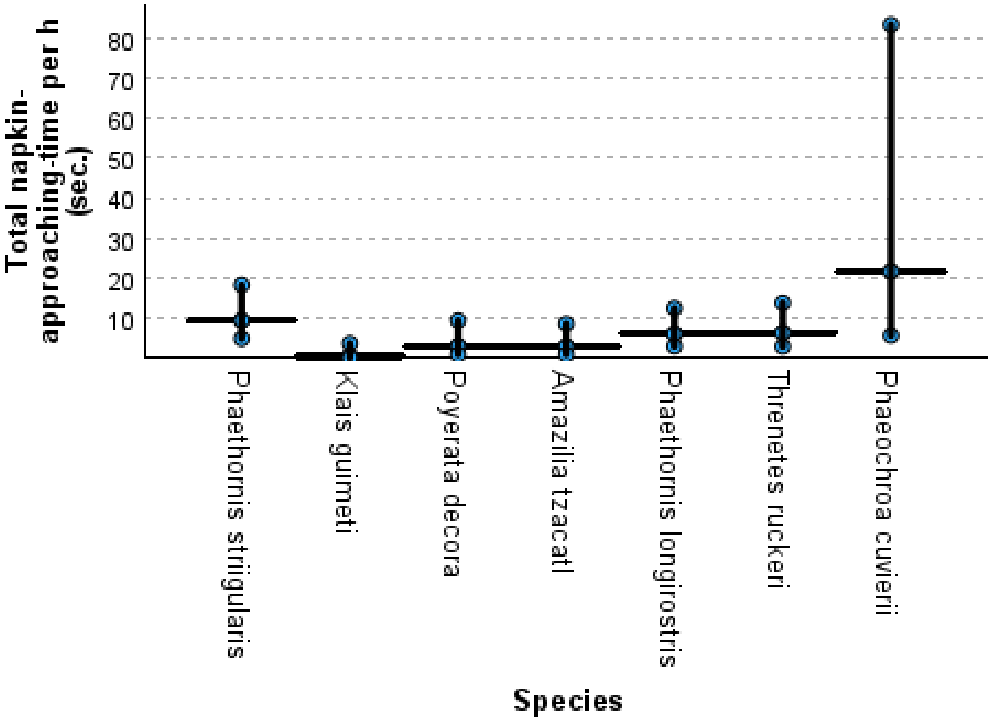


Fig. 4 Estimated mean of total duration (seconds per hour) (± 95% confidence intervals) spent by different hummingbird approaching (a) snake dummies, (b) mantis dummies and (c) napkins. Hummingbird species are sorted according to their weight (lightest species = left, heaviest species = right).

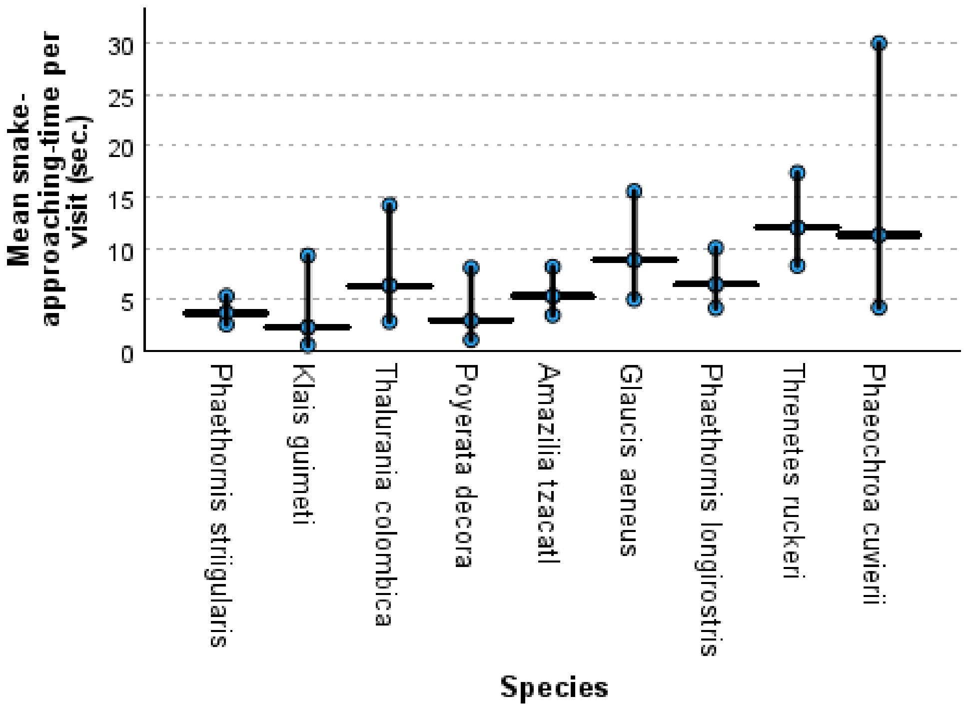
3.4 Mean predator approaching duration per visit

This section compares the mean approach times per hummingbird visit across the different treatments. In the snake treatment a significant effect of the fixed variable "bird species" ($p = 0.002$) was detected, meaning that the species behave differently. *Threnetes ruckeri* shows the highest average response to the snakes, while *Amazilia tzacatl* ($p = 0.008$), *Klais guimeti* ($p = 0.025$), *Phaethornis longirostris* ($p = 0.035$), *Phaethornis striigularis* ($p < 0.001$), and *Poyerata decora* ($p = 0.013$) exhibit a significantly shorter response time. *Glaucis aeneus* ($p = 0.370$), *Phaeochroa cuvierii* ($p = 0.905$), and *Thalurania colombica* ($p = 0.158$) showed no significant differences compared to *Threnetes ruckeri* (Fig. 5a).

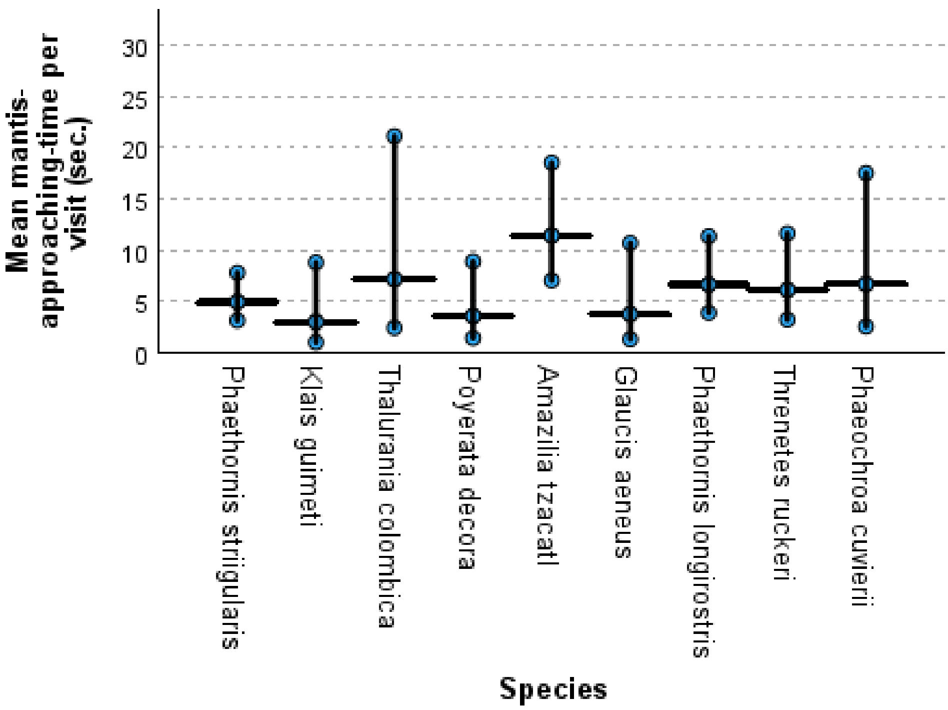
In contrast, the treatment mantis showed no significant effect, indicating that the different species do not behave significantly differently. Likewise, in the pairwise comparison with *Threnetes ruckeri*, no significant differences are observed, which is consistent with the results for the total time per hour (Fig. 5b).

In the napkin dataset a significant effect (p = 0.008) was found, indicating that the species exhibited different average reaction times per plant visit. Specifically, *Klais guimeti* (p = 0.001) and *Poyerata decora* (p = 0.042) spent significantly less time investigating the napkins compared to the reference species *Threnetes ruckeri*. No significant differences were found between *Threnetes ruckeri* and *Amazilia tzacatl* (p = 0.159), *Phaeochroa cuvierii* (p = 0.530), *Phaethornis longirostris* (p = 0.910), and *Phaethornis striigularis* (p = 0.463) (Fig. 5c).

(a)



(b)



(c)

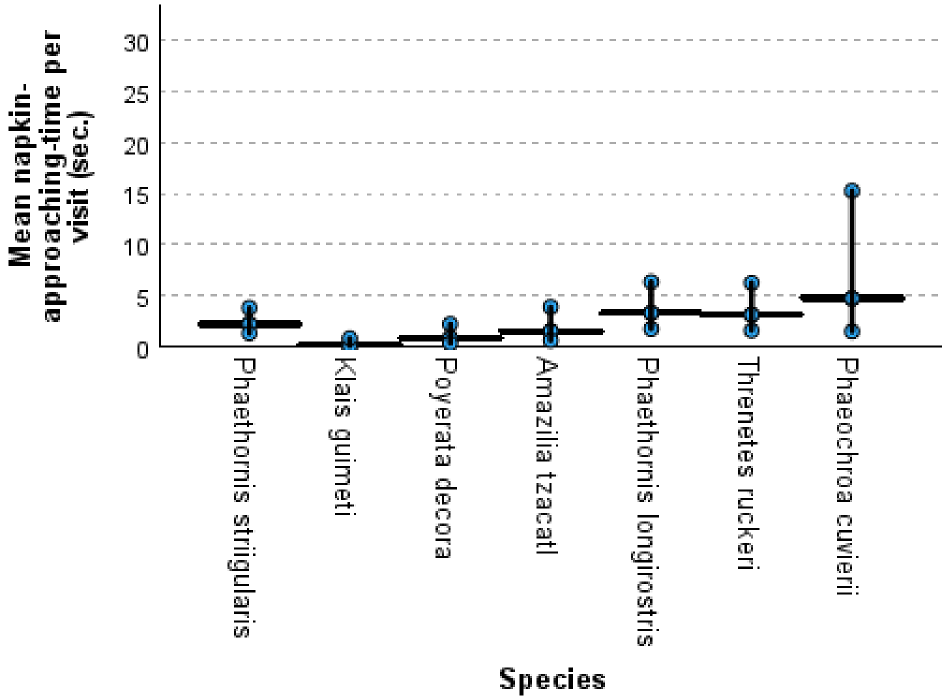


Fig. 5 Estimated mean value chart of the mean seconds spend approaching (a) snake dummies, (b) mantis dummies and (c) napkins per hour for each hummingbird species sorted by weight (lightest species = left, heaviest species = right). (± 95% confidence intervals)

3.5 Predator approaching duration per 60 seconds visit duration

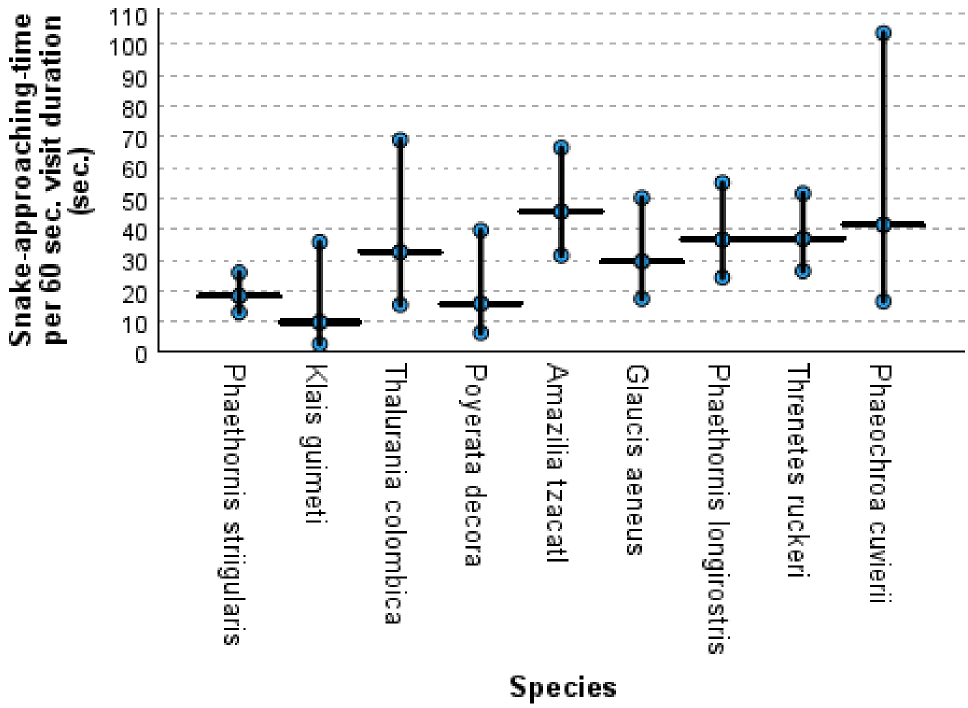
To ensure better comparability of the data, hummingbird approach times were adjusted to a 60-second plant visit interval in this analysis. A significant effect for the snake treatment was found for the fixed variable “bird species” ($p = 0.016$), suggesting that the species do significantly differ in their response to the snakes (Fig. 6a).

No significant effect was found in the mantis group for the fixed variable “bird species” ($p = 0.469$). This means that the different species do not exhibit significant differences in their predator approaching time when calculated per 60 seconds of plant visitation. Additionally, no significant differences were observed when each species was individually compared to the reference group *Threnetes ruckeri* (Fig. 6b).

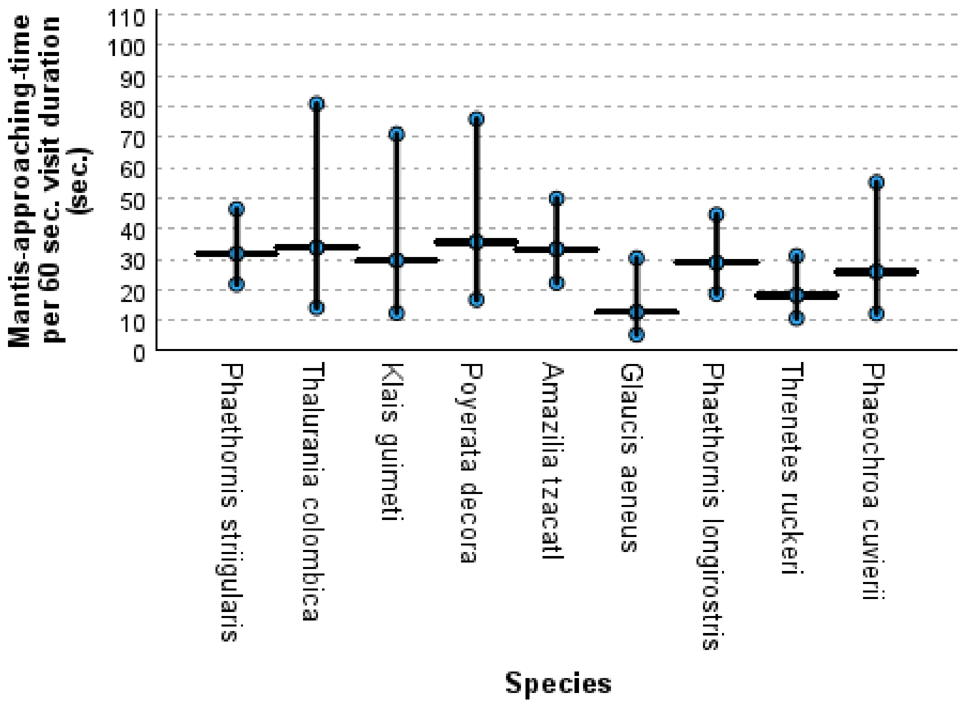
In contrast, the napkins showed a significant effect ($p < 0.003$). Specifically, *Klais guimeti* ($p < 0.001$) and *Poyerata decora* ($p = 0.010$) exhibited significantly lower values compared to *Threnetes ruckeri*, while no significant differences were found for *Amazilia tzacatl, Phaeochroa cuvierii, Phaethornis longirostris* and *Phaethornis striigularis* (Fig. 6c).

The y-axis is standardized to 60 seconds, corresponding to the maximum possible observation duration per visit. Values exceeding 60 seconds in the figure arise from the display of confidence intervals and represent statistical variability around the mean, not actual recorded measurements.

(a)



(b)



(c)

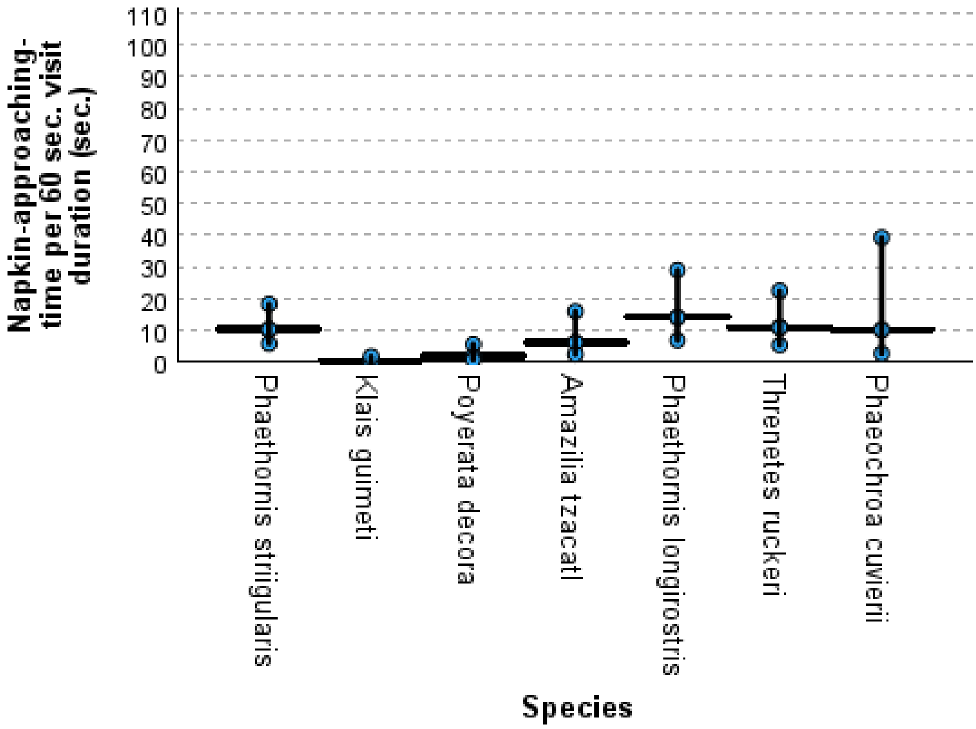


Fig. 6 Estimated mean value chart of duration spend approaching (a) snake dummies, (b) mantis dummies and (c) napkins scaled to one minute visit duration for each hummingbird species. (lightest species = left, heaviest species = right). (± 95% confidence intervals)

3.6 Predator approaching duration at first visit

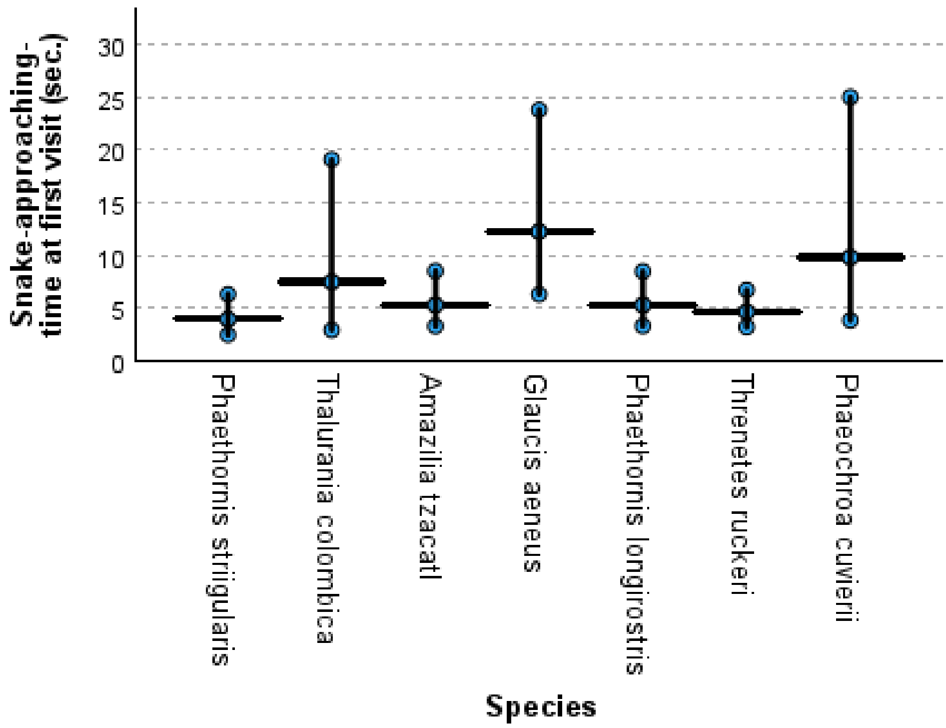
This section aims to examine whether there are differences in the hummingbirds' reactions during their first visit to the plant. The GLMM for the snake showed no significant effect of the fixed variable "bird species" ($p = 0.125$), meaning that the species behaved similarly during the first plant visit. However, *Glaucis aeneus* showed a significant difference ($p = 0.015$), spending more time approaching the snake than the reference species *Threnetes ruckeri* (Fig. 7a).

For the second predator, the praying mantis, the effect of the fixed variable "bird species" was marginally non-significant with $p = 0.058$, suggesting potential but not definitive differences between the species. However, individual species did not show significant deviations compared to the reference group *Threnetes ruckeri* (Fig. 7b).

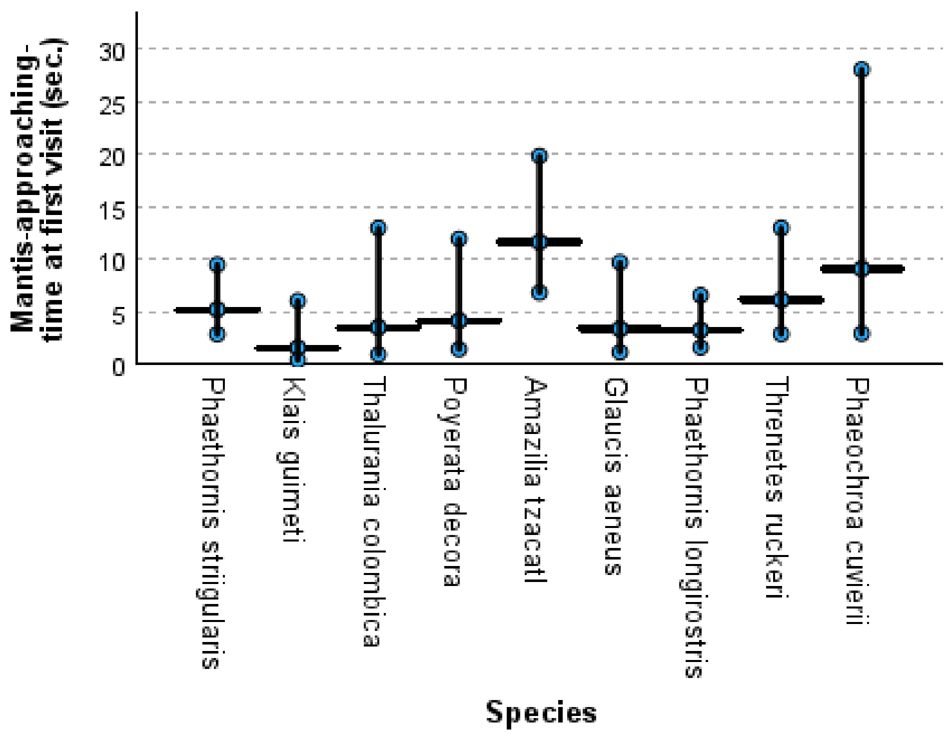
In the case of the third treatment (napkins), the corrected model was overall significant ($p = 0.021$), as was the factor "bird species" ($p = 0.020$). Here, *Phaethornis longirostris* showed a significantly shorter predator approaching duration (p =

0.024), while *Phaeochroa cuvierii* exhibited a marginal effect (p = 0.057). No significant differences were found for the other species (Fig. 7c).

(a)



(b)



(c)

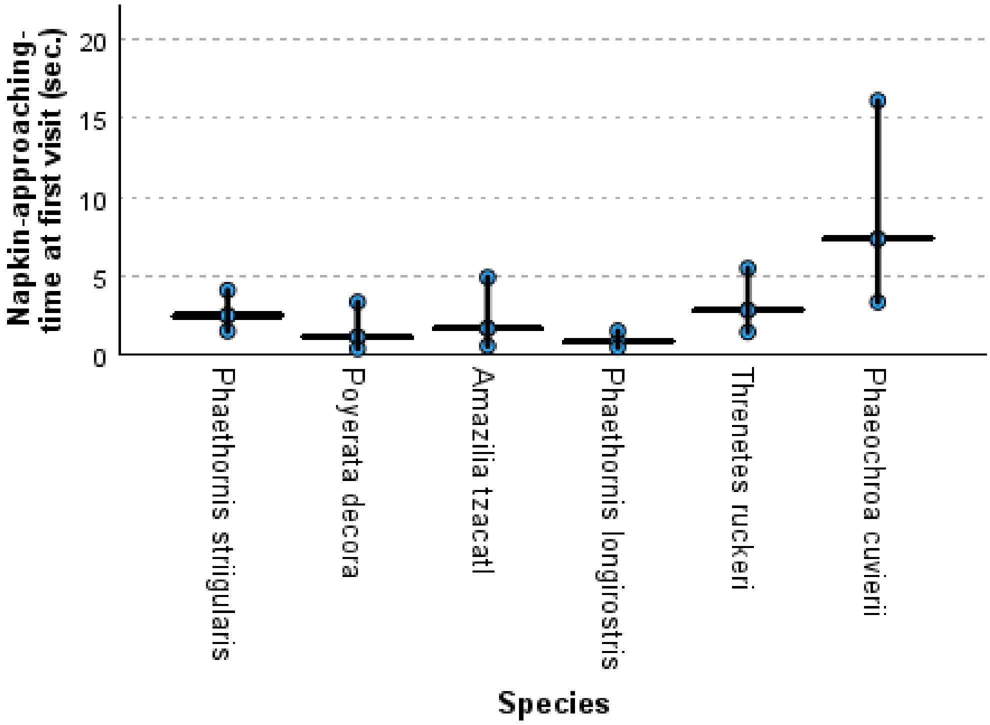


Fig. 7 Estimated mean value chart of the duration spend approaching (a) snake dummies, (b) mantis dummies and (c) napkins at the first flower visit in the second hour for each hummingbird species sorted by weight (lightest species = left, heaviest species = right). (± 95% confidence intervals)

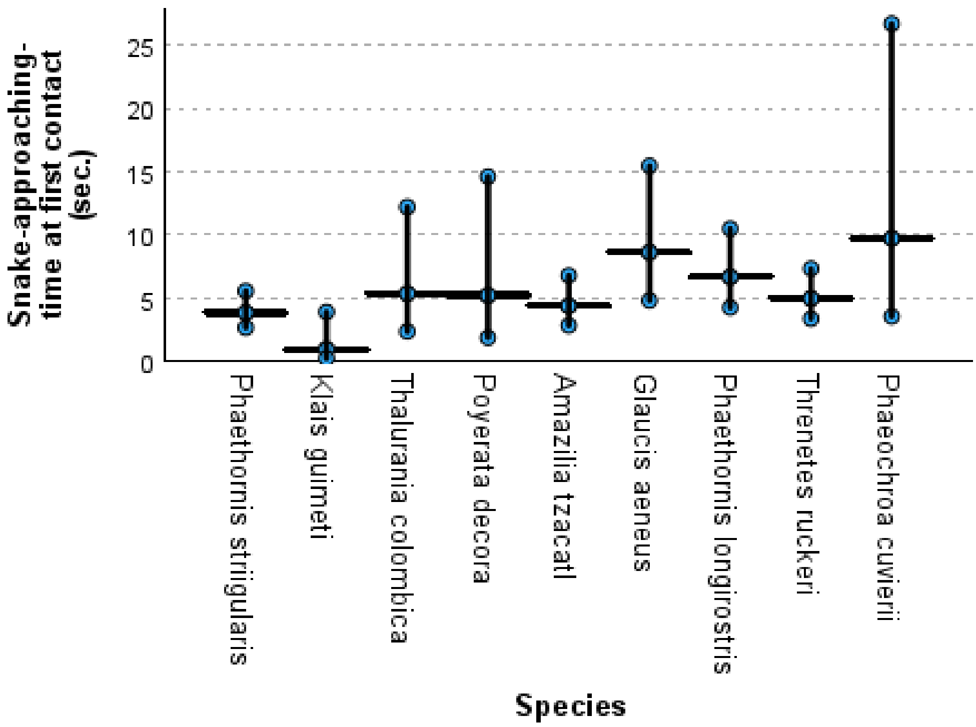
3.7 Predator approaching duration at first contact

In contrast to the previous section, the focus here was not on the first visit to the plant but on the first actual reaction to the treatment. The snake dummies showed no significant effect for the fixed variable “bird species” ($p = 0.084$). However, *Klais guimeti* showed a significant difference ($p = 0.027$) and spent significantly less time on the first contact with the predator compared to *Threnetes ruckeri*, while all other species showed no significant differences ($p > 0.05$) (Fig. 8a).

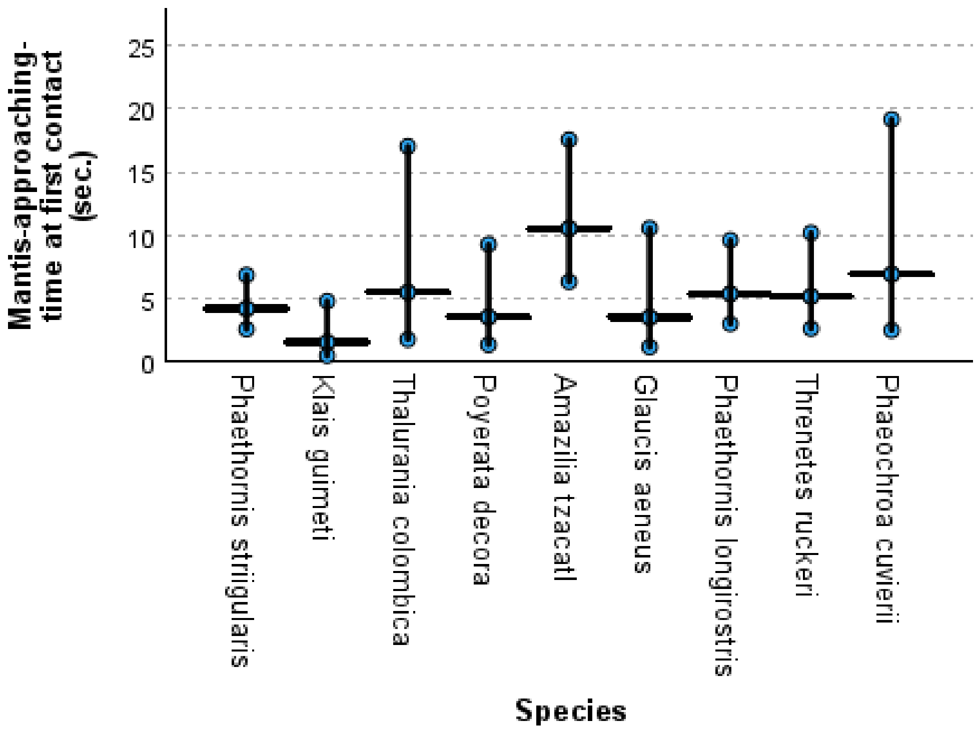
A similar pattern was observed in the praying mantis treatment. The GLMM again showed no significant effect for “bird species” ($p = 0.084$), and the analysis of individual species also revealed no significant differences compared to the reference group *Threnetes ruckeri* (Fig. 8b).

Similarly, in the napkins experiment, the factor “bird species” ($p = 0.063$) had no significant effect on the duration of the first reaction to the predator. No significant differences to the reference group were found here either (Fig. 8c).

(a)


Snake-approaching-time at first contact (sec.)
0
5
10
15
20
25
Phaethornis striigularis
Klais guimeti
Thalurania colombica
Poyerata decora
Amazilia tzacatl
Glaucis aeneus
Phaethornis longirostris
Threnetes ruckeri
Phaeochroa cuvierii
Species

(b)


Mantis-approaching-time at first contact (sec.)
0
5
10
15
20
25
Phaethornis striigularis
Klais guimeti
Thalurania colombica
Poyerata decora
Amazilia tzacatl
Glaucis aeneus
Phaethornis longirostris
Threnetes ruckeri
Phaeochroa cuvierii
Species

(c)

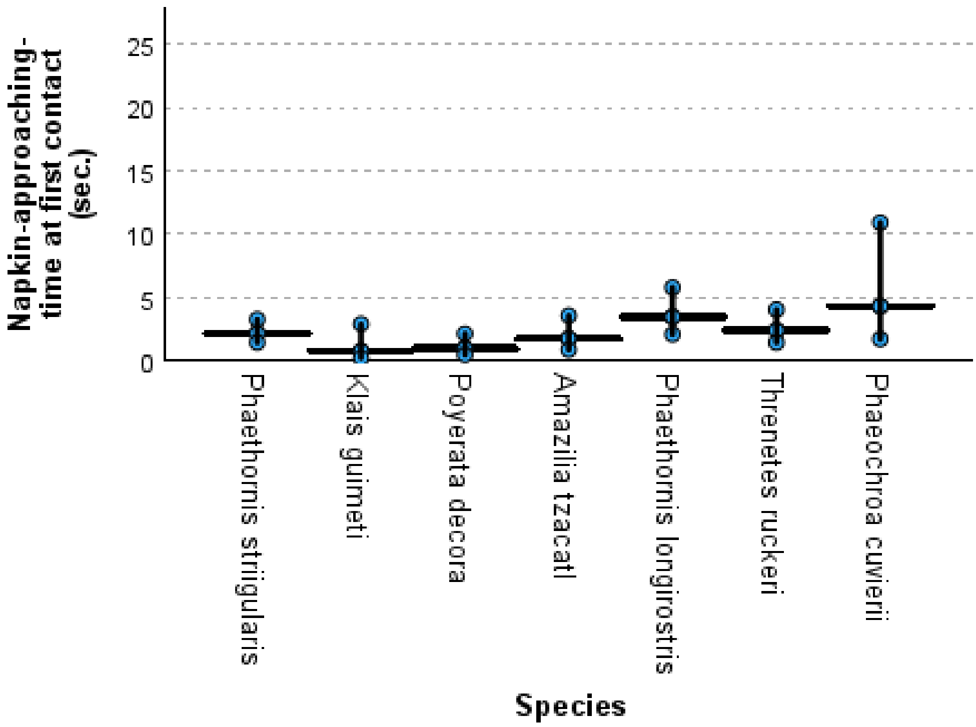


Fig. 8 Estimated mean value chart of the duration spend approaching (a) snake dummies, (b) mantis dummies and (c) napkins at the first sight of the snakes in the second hour for each hummingbird species sorted by weight (lightest species = left, heaviest species = right). (± 95% confidence intervals)

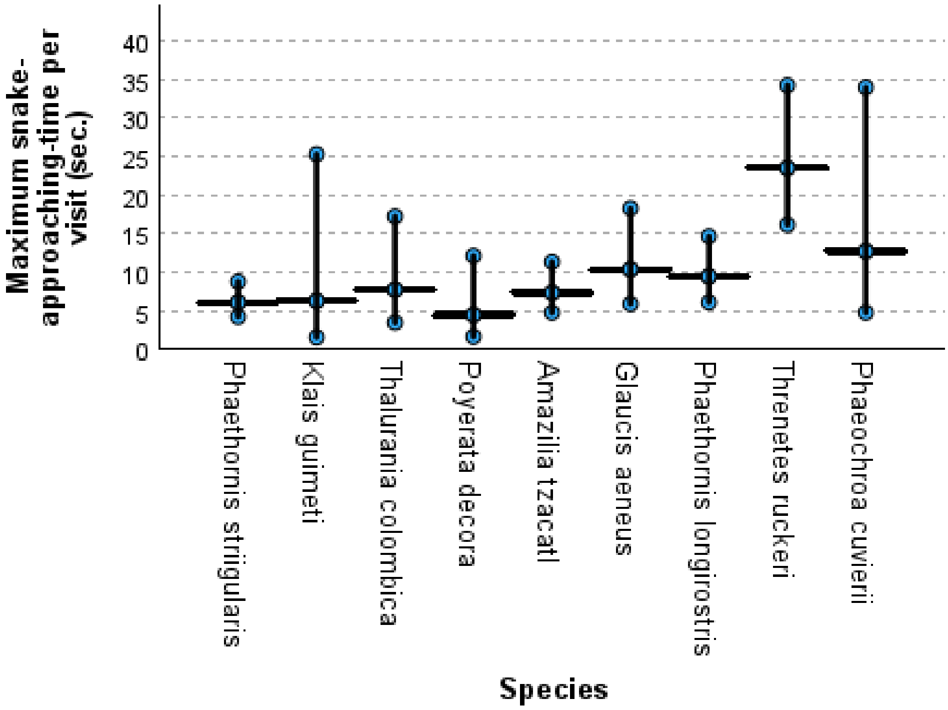
3.8 Maximum predator approaching duration per visit

This analysis compares the longest recorded reactions across the different treatments. In the case of the snake treatment a significant effect of the fixed variable "bird species" ($p < 0.001$) was found, suggesting that the species differ in their maximum predator approaching time. *Threnetes ruckeri* showed significant differences compared to *Amazilia tzacatl* ($p < 0.001$), *Glaucis aeneus* ($p = 0.020$), *Phaethornis longirostris* ($p = 0.003$), *Phaethornis striigularis* ($p < 0.001$), *Poyerata decora* ($p = 0.003$), and *Thalurania colombica* ($p = 0.015$), while no significant differences were found for *Klais guimeti* ($p = 0.070$) and *Phaeochroa cuvierii* ($p = 0.250$). This indicates that *Threnetes ruckeri* has a higher maximum predator approaching time than most other species (Fig.9a).

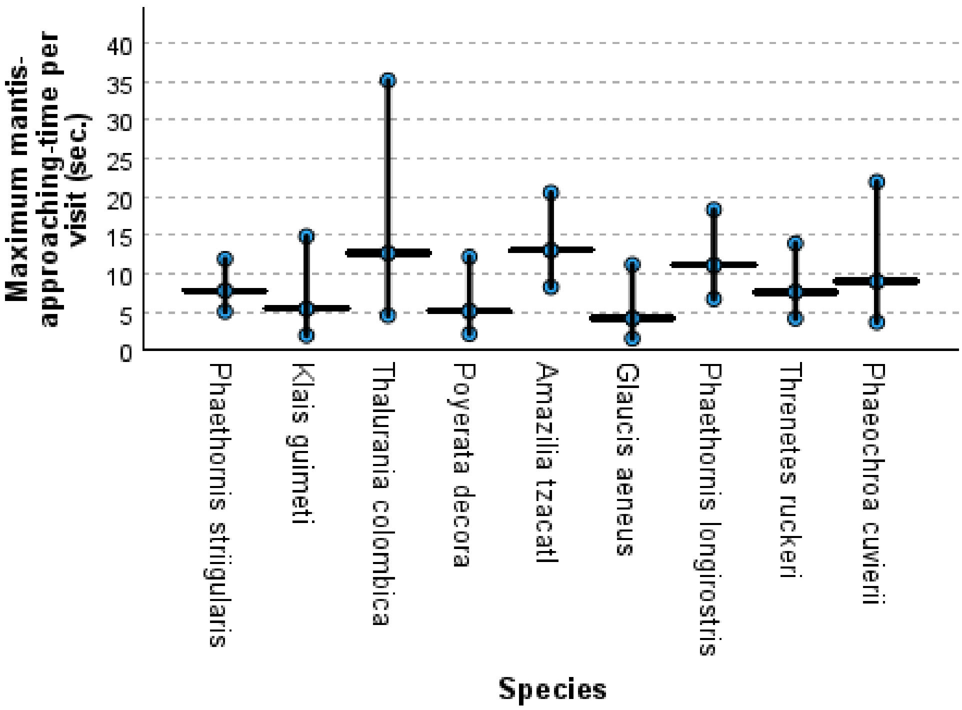
On the other hand, for the mantis treatment, no significant effect of the fixed variable "bird species" ($p = 0.297$) was detected, indicating that the species did not differ significantly in their maximum response to the treatment. Furthermore, no significant differences were found when compared to the reference group *Threnetes ruckeri* (Fig. 9b).

For the napkins, the corrected model showed a significant overall effect (p = 0.036), although the influence of the species was marginally (p = 0.059). When examining the fixed coefficients, *Klais guimeti* showed a significantly lower maximum predator approaching time (p = 0.014) than *Threnetes ruckeri* (Fig. 9c).

(a)



(b)



(c)

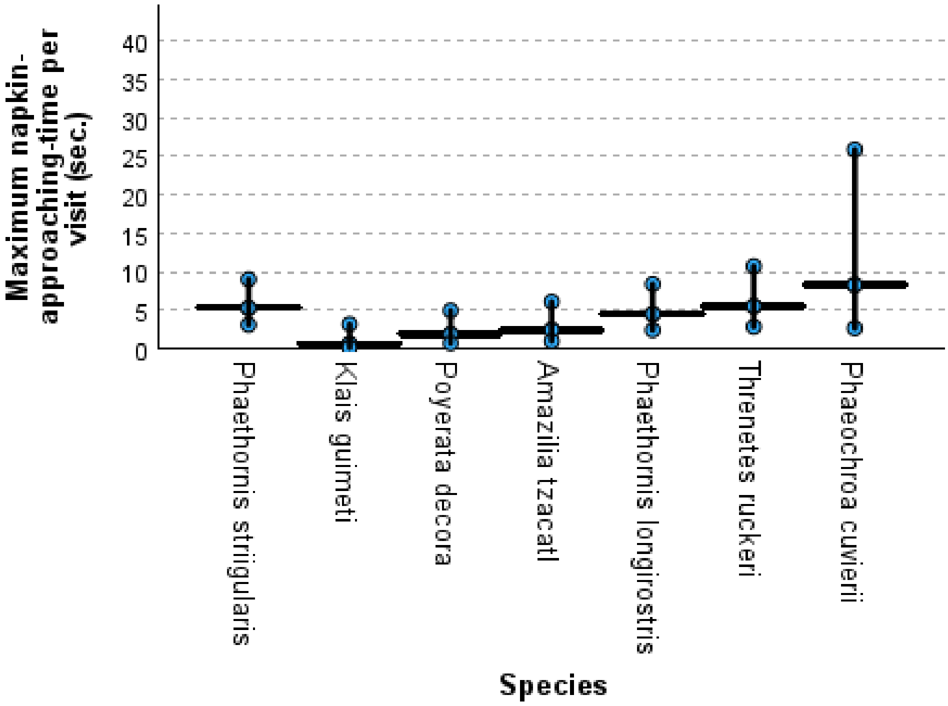


Fig. 9 Estimated mean value chart of the maximum duration spent approaching (a) snake dummies, (b) mantis dummies and (c) napkins for each hummingbird species sorted by weight (lightest species = left, heaviest species = right). (± 95% confidence intervals)

3.9 Comparison of no reaction rates

To determine whether there is a relationship between the frequency of reactions to the different treatments and hummingbird species, the proportion of no reactions in the treatment data was analysed. No correlation between hummingbird species and the frequency of reactions was identified. However, in the following species, the proportion of reactions increased with the perceived threat level of the treatment: *Phaethornis strigularis, Klais guimeti, Amazilia tzacatl, Glaucis aeneus*, and *Threnetes ruckeri*. For *Thalurania colombica*, no comparative values were available for the first hour. In *Poyerata decora*, reactions increased when comparing the napkin treatment to the predator treatment. Furthermore, this species responded more frequently to mantises than to snakes. In *Phaethornis longirostris*, the number of reactions rose from the napkins to the predator treatments but remained nearly constant among the different predators. *Phaeochroa cuvierii* was the only species that consistently reacted to the napkins but responded less frequently to mantises and snakes (Fig 10).

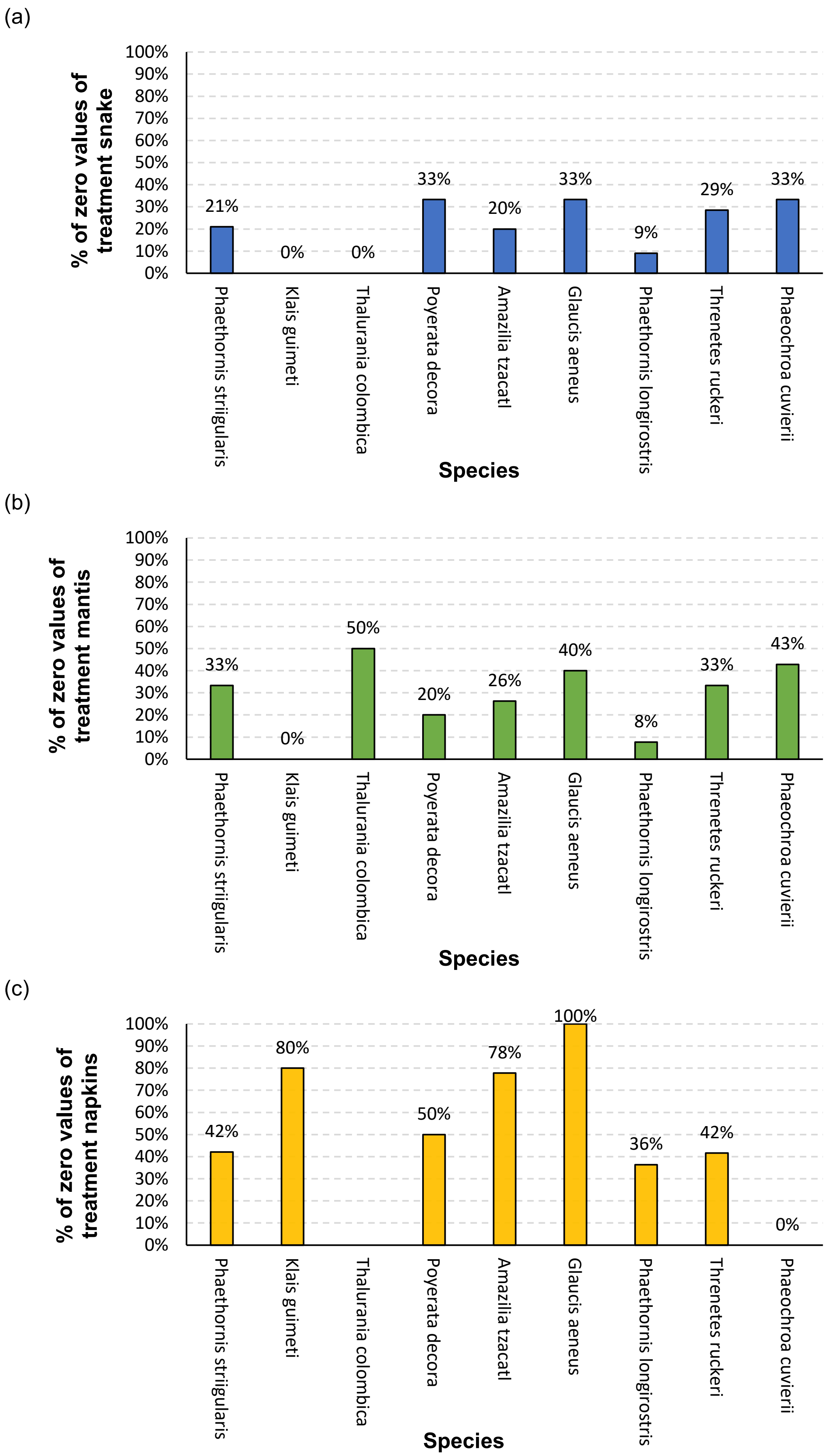


Fig. 10 The percentage of no reactions on (a) snake dummies, (b) mantis dummies and (c) napkins. Hummingbird species are sorted by weight (lightest species = left, heaviest species = right).

3.10 Comparison of visit duration

In the following the mean visit duration per hour for the second observation period has been compared in the three treatments. According to the GLMM the difference between the treatments snake and napkins is not significant (p = 0.378) (Fig. 11).

No species-specific patterns were identified, except for the largest species, *Phaeochroa cuvierii*. This species exhibited an increase in visit duration as the perceived threat level decreased. Additionally, this species had the longest overall average flower visit duration in the presence of mantises and napkins (Fig. 12).

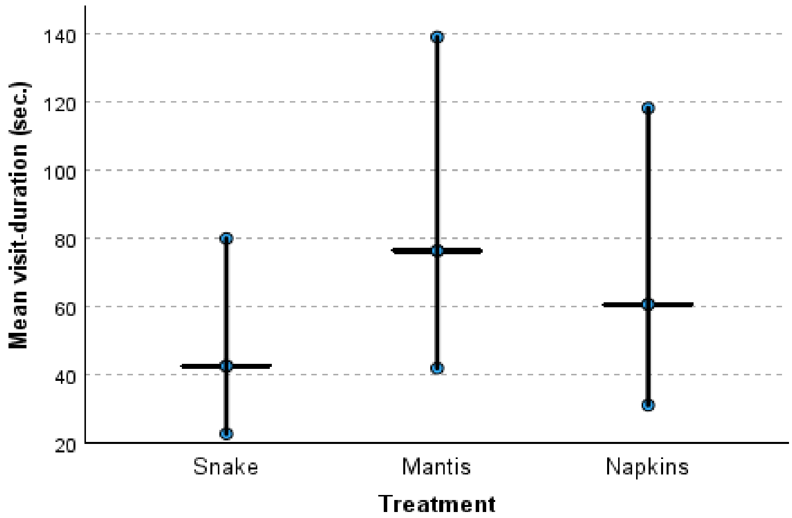


Fig. 11 Mean visit duration of the second observation hour grouped in the three treatments (snake, mantis and napkins). (± 95% confidence intervals)

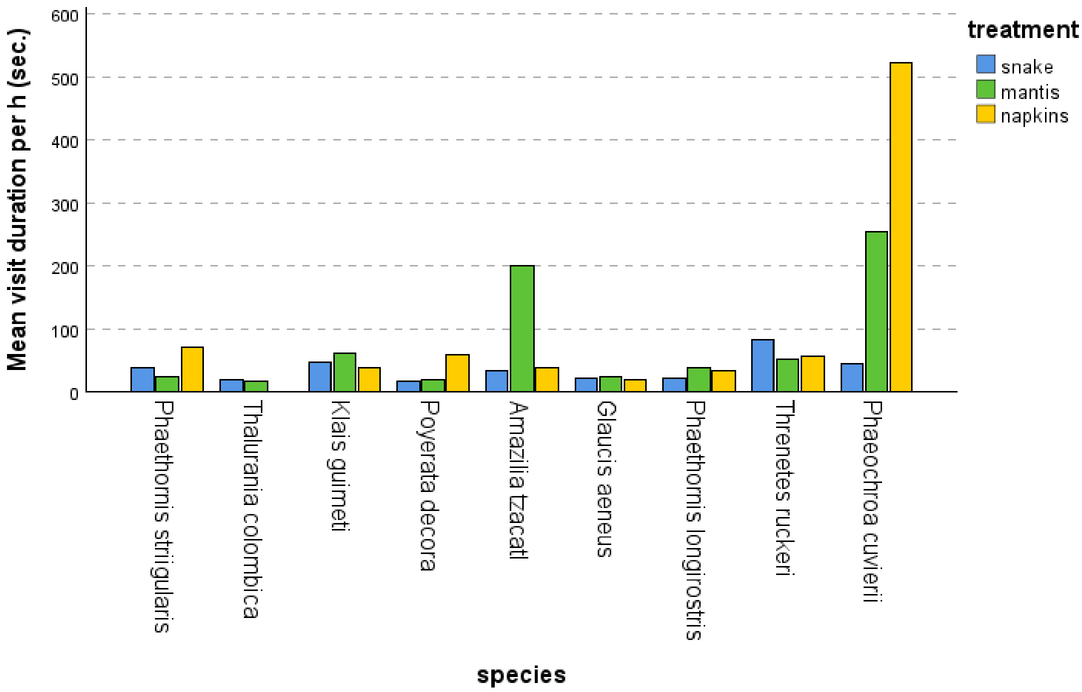


Fig. 12 Comparison of the mean flower visit duration of the second filming hour across the three treatments (snake, mantis, napkin). (lightest species = left, heaviest species = right).

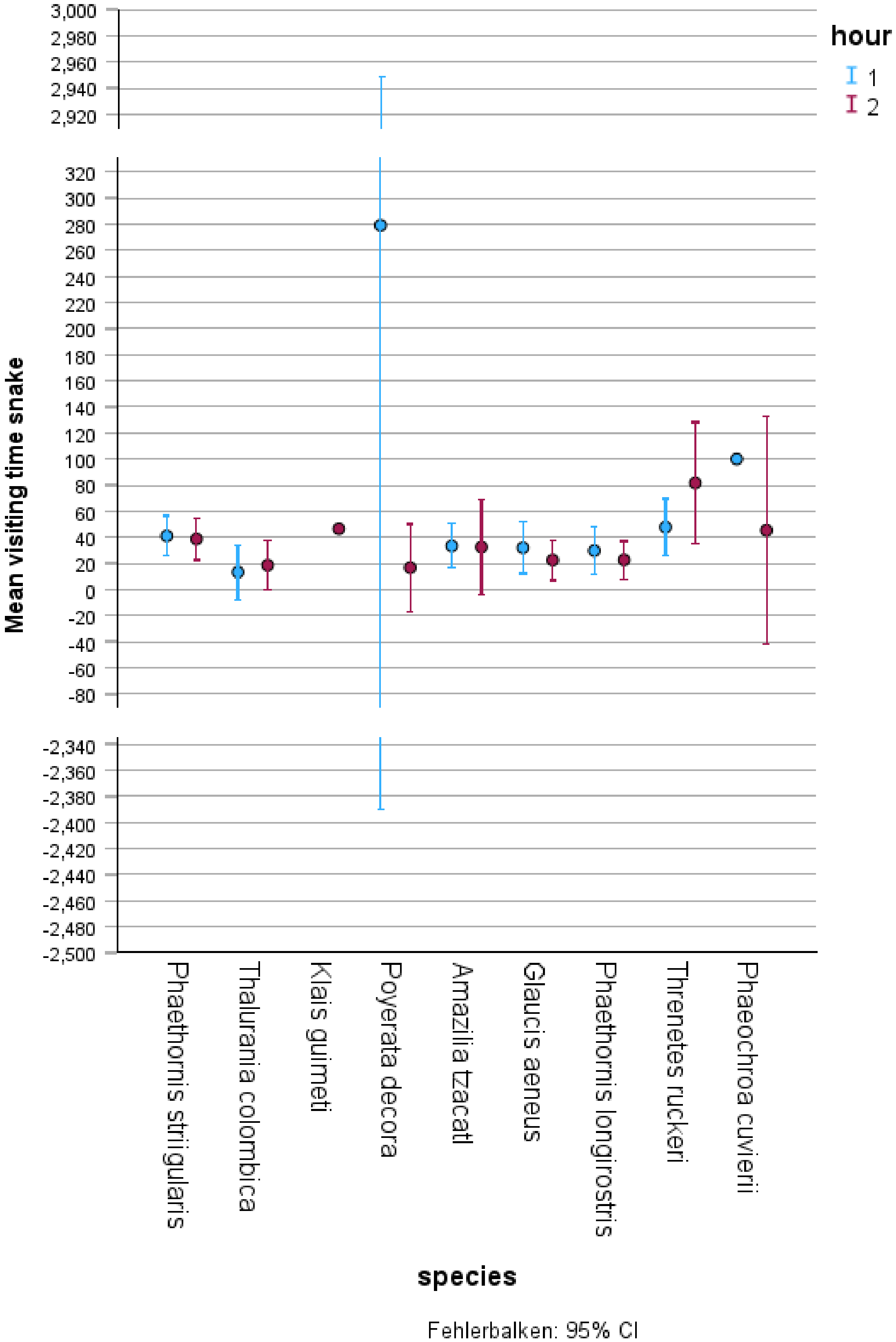
Comparing the visit duration per hour in the first hour (without manipulation) and second hour (with treatments), grouped by species in the snake treatment, only small differences can be found in *Phaethornis striigularis, Thalurania colombica, Amazilia tzacatl, Glaucis aeneus*, and *Phaethornis longirostris*. For *Klais guimeti*, comparative data for the first hour are missing. In *Poyerata decora* and *Phaeochroa cuvierii*, flower visit duration decreases in the presence of the snake. Interestingly, in *Threnetes ruckeri*, flower visit duration increases in the second hour (Fig. 13a).

In the experiment involving the praying mantis dummies, no remarkable differences in flower visit durations were observed for *Phaethornis strigularis*, *Klais guimeti*, *Thalurania colombica*, *Amazilia tzacatl*, *Glaucis aeneus*, *Phaethornis longirostris*, and this time also for *Threnetes ruckeri*. For *Poyerata decora*, the flower visit time was once again significantly shortened in the second hour. For *Phaeochroa cuvierii*, the flower visit time increased sharply in the second hour (Fig. 13b).

In the two documented cases of *Phaeochroa cuvierii*, flower visit duration in presence of the napkins increased markedly in the second hour. *Phaethornis striigularis* also exhibited a slight increase in visit duration during the second hour. No noticeable differences were observed in the other species (Fig 13c).

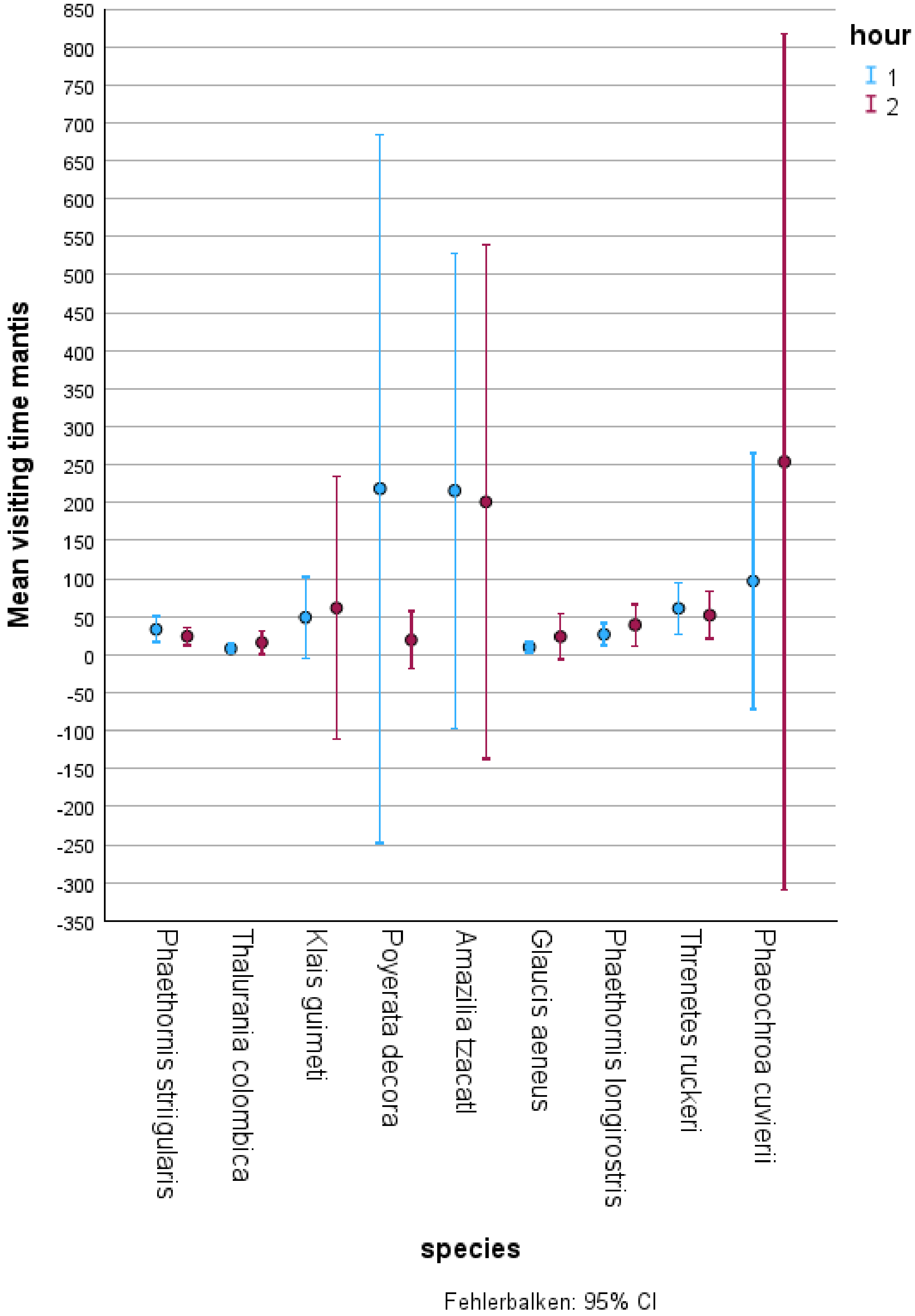
The high apparent outliers in the figure are due to wide confidence intervals (CI) caused by small sample sizes in some species. This increases uncertainty and should be kept in mind when interpreting the data.

(a)



hour
1
2
Mean visiting time snake
3,000
2,980
2,960
2,940
2,920
320
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0
-20
-40
-60
-80
-2,340
-2,360
-2,380
-2,400
-2,420
-2,440
-2,460
-2,480
-2,500
Phaethornis striigularis
Thalurania colombica
Klais guimeti
Poyerata decora
Amazilia tzacatl
Glaucis aeneus
Phaethornis longirostris
Threnetes ruckeri
Phaeochroa cuvierii
species
Fehlerbalken: 95% CI

(b)


hour
1
2
Mean visiting time mantis
850
800
750
700
650
600
550
500
450
400
350
300
250
200
150
100
50
0
-50
-100
-150
-200
-250
-300
-350
Phaethornis striigularis
Thalurania colombica
Klais guimeti
Poyerata decora
Amazilia tzacatl
Glaucis aeneus
Phaethornis longirostris
Threnetes ruckeri
Phaeochroa cuvierii
species
Fehlerbalken: 95% CI

(c)

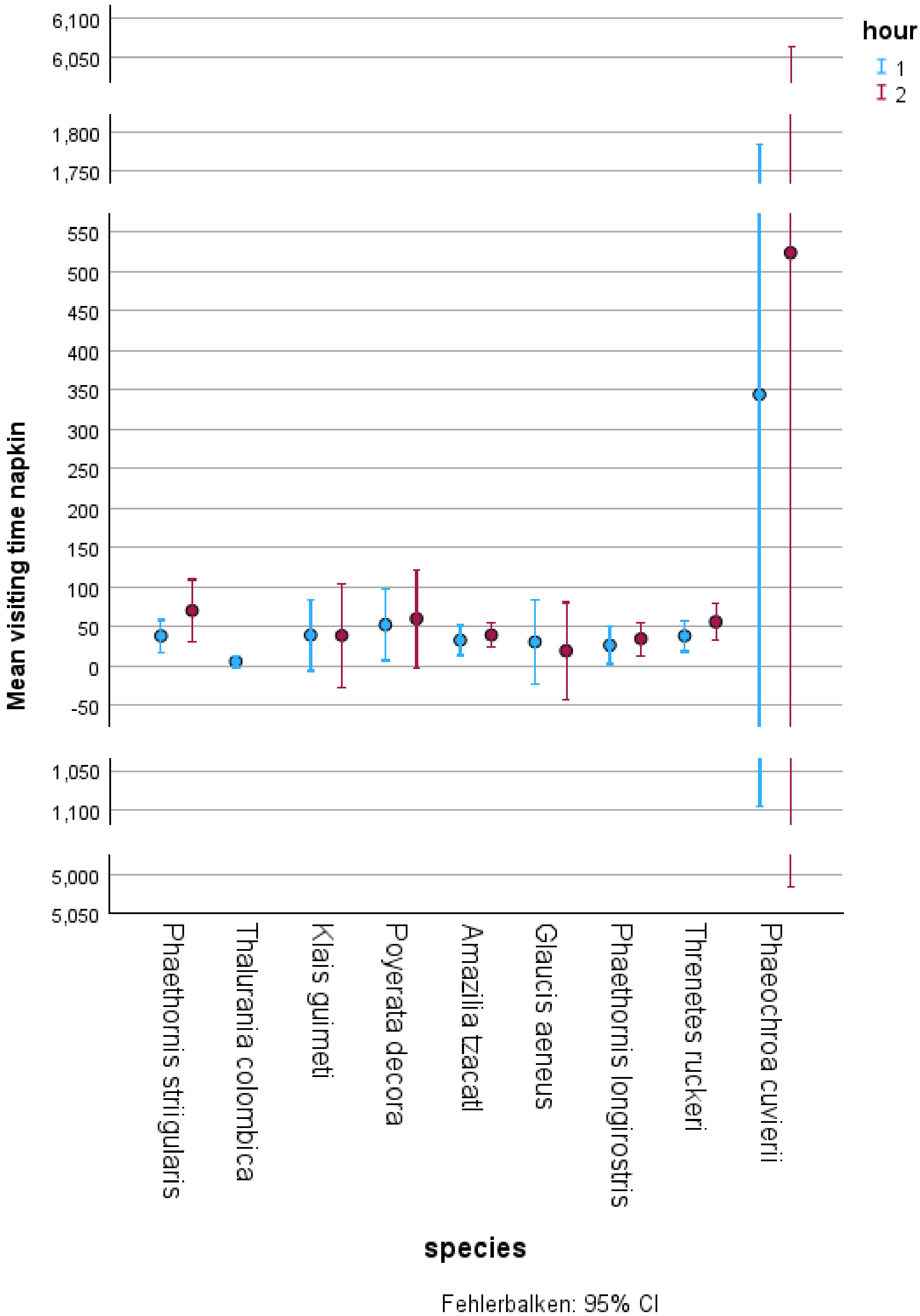


Fig. 13 Comparison of the mean visit duration for the treatment (a) snake dummies, (b) mantis dummies and (c) napkins in the first and second hour grouped in hummingbird species. (±95% CI)

4 Discussion

The results indicate a significant response of the hummingbirds to the predator dummies. This response was expressed through varying intensities of behaviour, such as spreading their tail feathers and inspecting the dummies from multiple angles. Occasionally, individuals returned after a short time to hover around the dummies again. Although attacking behaviour during foraging has been reported in previous studies (Gloudeman & Eberts, 2017; West & Butler, 2010), no such behaviour was observed in the present study. Similar responses have been reported in other experiments using predator dummies to investigate hummingbird foraging behaviour (Lai, 2010). These observations suggest that hummingbirds recognize the snake and mantis dummies as potential predators and, consequently, as a risk during foraging. The effectiveness of predator dummies for behavioural observations in birds is further supported by studies investigating nest-defence strategies using snake models (Ellison & Ribic, 2012) as well as the effects of owl models on foraging behaviour (Rensel & Wilder, 2012). Furthermore, the present results clearly demonstrate that hummingbirds can distinguish between neutral objects (e.g. napkins) and potential predators. Treatment approaching time was almost twice as long when hummingbirds were exposed to snakes and praying mantises compared to napkins.

A crucial limitation of all GLMM analyses is that data points with no reaction to snakes, mantises, or napkins were excluded. This is particularly relevant for the napkin treatment, where in 40 out of 75 cases (53.33%), no reaction occurred. This underlines that the napkins weren't perceived as a threat to the hummingbirds. In the praying mantis treatment, there was no reaction in 27 out of 94 cases (28.72%), and in the snake treatment, no reaction was observed in 19 out of 85 cases (22.35%). Although, the dataset is in some cases too small to draw meaningful conclusions about species, a slight increase in reactions can be observed with rising threat intensity across the whole dataset.

When examining the foraging of snakes, the size of the prey is an important limitation. There is no doubt that small birds are suitable prey for snakes, which results in a high risk in the presence of a snake for all studied hummingbird species (Ellison & Ribic, 2012; Henderson, 2023; Littlefield, 2007; Mise *et al.,* 2021; Siers *et al.* ,2025). Interestingly, the two largest species, *Threnetes ruckeri* and *Phaeochroa* *cuvierii*, exhibited the longest maximum reaction time to the snakes, although the small sample size of *Phaeochroa cuvierii* limits firm conclusions. Nevertheless, the second largest species, *Threnetes ruckeri,* with sufficient data, showed by far the longest average reaction to snakes per hour (45.51 seconds) and flower visit duration even increased in the presence of the snake dummies.

In the praying mantis treatment, no significant differences between species were detected, but clear behavioural changes were still observed. Comparable findings have been reported in other studies testing arthropods as threat models. For example, a study using the bullet ant (*Paraponera clavata*) as a perceived threat showed a reduced foraging efficiency of *Phaethornis longirostris* (Wojczulanis-Jakubas & Araya-Salas, 2023). Another study that observed feeding behaviour in hummingbirds in the presence of wasps also reported increased alertness and wasp avoidance (Carr & Golinski, 2020). Further evidence of the predatory risk posed by arthropods is provided by reports of observed predation events: a tailless whipscorpion (*Phrynus longipes*) was observed feeding on an Antillean crested hummingbird (*Orthorhyncus cristatus*) (Owen & Cokendolpher, 2006), also some reports describe hummingbirds as a prey of mantises (Lorenz, 2007; Nyffeler *et al.*, 2017). Similar to the snake observation, there could also be noted an increase in flower visit duration in the presence of the praying mantises. This time, however, it occurs in the largest species, *Phaeochroa cuvierii*. A comparable increase in visit duration was also observed in this species during the napkin treatment. Furthermore, *Threnetes ruckeri* showed an increased flower visit duration in the presence of snakes. Since *Threnetes ruckeri* and *Phaeochroa cuvierii* are the two largest species analysed, this pattern could indicate that larger species either exhibit greater aggressiveness toward predators or perceive the predators as less threatening, resulting in longer plant visits. However, it should be noted that for *Phaeochroa cuvierii*, there were only three recorded cases in the snake treatment and two in the napkin treatment.

In contrast, one species exhibited the reverse response in terms of total flower visit duration. *Poyerata decora* showed a drastic reduction in the presence of predator dummies, suggesting that this hummingbird species is particularly cautious when dealing with predators. Since this species is neither among the smallest nor the largest, no correlation between its behaviour and body size was observed. Again, the sample size limits the interpretability of the results.

Several studies show different foraging and territorial behaviour between hermits and true hummingbirds (Ferreira *et al.*, 2006; Gill, 1988; Thiel *et al.,* 2021). Hermit species mainly search for food in the lower and middle forest layers, while true hummingbird species forage across the entire vertical gradient. Competition for food is an important factor in structuring the community. Niche separation occurs not only along the vertical gradient of a plant but also through specialization on specific plant species. Furthermore, hermit and true hummingbird species differ clearly in their feeding behaviour. True hummingbirds establish and defend territories, gaining exclusive access to flower clusters, whereas hermits, as trapliners, visit flowers along fixed routes in a regular sequence without defending territories (Thiel *et al*., 2021). These differences suggest that hermits and true hummingbirds may react differently to predators during foraging. In the present study, however, no significant differences in anti-predator behaviour between the two groups were detected.

Building on the previous findings, the following section explores how differences in body size among the tested hummingbird species may affect their behavioural responses to the predator dummies. While it is evident that a snake of the size used in the dummies could easily prey on a hummingbird, it remains unclear which hummingbird sizes are at risk from predation by praying mantises. It can be assumed that mantises pose a lower threat than snakes, but this depends on the predator's size. Records show a remarkably broad prey spectrum, ranging from arthropods to wall lizards (*Podarcis muralis*) (Wurmitzer & Kleewein, 2025), to horned vipers (*Vipera ammodytes*) (Stangl, 2025), and even hummingbirds (Lorenz, 2007; Nyffeler *et al*., 2017). Studies indicate that mantises up to 11 cm in size can be found in Costa Rica, for example *Macromantis nicaraguae* (De Luna *et al.,* 2024). In this study, large praying mantis models (11 cm) were used as predator dummies. The size of their prey can reach up to 110 % of their own body weight (Reitze & Nentwig, 1991). Assuming a large praying mantis weighs around 7 g, all tested hummingbird species except the largest, *Phaeochroa cuvierii,* would thus fall within its potential prey range (Nyffeler *et al.,* 2017). Based on this, it remains uncertain whether a mantis of this size actually poses a lower risk to hummingbirds than a snake. Indeed, the potential threat from a praying mantis might even be greater. Reports of snakes preying on hummingbirds are rare (Littlefield, 2007; Henderson, 2023). The results might have been more distinct if the perceived threat gradient had been increased by using smaller mantis dummies.

In summary, as the potential threat increases, the frequency and duration of hummingbird reactions tend to increase as well. Larger species may exhibit greater aggression toward the predators or perceive the predators as less threatening. These findings tentatively support the hypothesis that body size may correlate with reduced predator sensitivity behaviour. However, further data is required to confirm this pattern. No behavioural differences in response to the treatments could be observed between the subfamilies hermits and true hummingbirds.

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