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Investigating the Nocturnal Behavior of Zoo-Housed Tawny Frogmouths

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Abstract

The tawny frogmouth (*Podargus strigoides)* is an insectivorous bird found throughout Australia and Tasmania. The nocturnal habits of this species make them a challenging subject for wild behavioral research. Captive studies may therefore help to fill a knowledge gap in the 24-hour activity budget for this species. To investigate the behavior of captive frogmouths, we used nocturnal cameras on a pair, trio and group of five birds held at two zoological collections in the United Kingdom. Tawny frogmouths engaged in a range of inactive behaviors during the day such as huddling, roosting and sitting in a slouched position. During the night, however, active behaviors such as head bobbing and flight were observed much more frequently. Behavior also varied between groups, with the pair of birds spending more time engaged in observations of their environment. This indicates that life stage and social grouping also have an impact on behavior. Weather conditions had limited impact on frogmouth behaviour.

This study suggests that tawny frogmouths retain their nocturnal activity budget, even in the captive environment where visitor presence and feeding regimes might encourage diurnal activity. The data also represents the first 24-hour activity budgets for frogmouths, and as such could be used by researchers to investigate the effects of husbandry practices such as enrichment provision.

Research highlights

Tawny frogmouths showed significantly more active behaviors outside of daytime observation.

During night observations, tawny frogmouths displayed a range of behaviors including head bobbing.

Frogmouth social grouping was a significant predictor of differences in posture and head bobbing behavior.

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Introduction

Behavioral observations can help researchers to better understand the breeding requirements, habitat preferences and diets for animals [1]. A more informed understanding of animal behavior can help in developing husbandry practices for captive animals or put in place conservation measures for endangered species [2].

The tawny frogmouth (*Podargus strigoides)* is a predatory bird endemic to Australia and Tasmania [3]. Described as Least Concern by the International Union for Conservation of Nature [4], the species appears to be able to survive around human habitation [5]. Despite its owl-like appearance, *P. strigoides* belongs to the Caprimulgiformes Order; a taxon that includes nightjars, swifts and potoos [6]. *P. strigoides'* diet reflects this: The species is generally insectivorous, and vertebrate prey is believed to make up only a minor component of the wild diet [7,6, 8].

P. strigoides have been the subject of considerable research interest in the wild and in laboratories [3,9,12]. The metabolic rate, which is only 60% of the predicted value for non-passerine birds, has received considerable research attention [2,9]. This reduced metabolic rate may be related to the insect-based diet of the species, as insects are comparatively low in energy [3]. In the wild, *P. strigoides* make use of several energy saving mechanisms, including torpor and long periods of inactive behavior [10,11,12].

Several behavior and habitat use studies have also been conducted: *P. strigoides* is often inactive during the day and makes use of cryptic coloration and postures to reduce predation risk [10,11]. The species is often found in association with *Eucalyptus spp.* trees, where its coloration acts particularly effectively as camouflage [13]. The species is reported to be crepuscular, though may sometimes be active during the night [6,14]. However, quantitative information on frogmouth nocturnal behavior is currently limited to sightings during surveys. Nocturnal study of wild bird behavior remains a challenging area of study due to difficulties with lighting, tracking, and potential disruption of the normal behavior of study subjects. However, studies on other species, such as wild greater flamingos (*Phoenicopterus roseus)* have been valuable in better understanding relationships between vigilance and predation risk [15].

Given their solitary behavior and cryptic coloration, behavior studies on frogmouths that incorporate dusk, night and dawn are likely to be more challenging to develop than those used for flamingos. Behavioral research using a 24-hour time frame on *P. strigoides* may have value in filling in a current knowledge gap in zoo biology.

Nocturnal study of zoo animals

Historically, the majority of captive animal behavior studies have investigated animal behavior during zoo opening hours [2], despite the fact that many species are crepuscular or nocturnal in nature. With many studies falling within an eight-hour daytime window or less, 60% of the activity budget of captive subjects may remain unexplored. Recently, greater exploration of the 24-hour captive animal activity budget has been undertaken, with studies investigating the nocturnal behavior of greater flamingos [16], primates [17,18], giraffes (*Giraffa camelopardis)* [19] and elephants (*Loxodonta africana* and *Elephas maximus)* [20,21]. Currently, however, nocturnal behavior studies are still comparatively rare, and tend to be more common for large, charismatic mammalian species [20,22, 19].

Early studies of animal behavior were limited by observer availability and zoo opening hours [17]. However, improvements in camera technology have made nocturnal observations more feasible, removing the requirement for an observer to be present [20]. The use of cameras to observe behavior may minimize observer effects and build a more holistic, less day-focused understanding of behavior.

P. strigoides is housed in at least 150 zoological collections globally, with over 300 individuals in captivity, according to the Zoological Information Management System (ZIMS) [23]. Despite its prevalence in zoos, this species has been the focus of relatively few zoo-based studies. *P. strigoides* is also held in a range of different social groupings, with some zoos and wildlife centers holding single individuals, or housing related individuals in small groups [23].

Further behavioral studies on this species would be valuable from two perspectives: first, *P. strigoides* is difficult to observe in its wild state at night, hampering the ability of researchers to assess the normal nocturnal behavior of wild birds in a standardized format (e.g. activity budget) [6]. As a result, there are currently no published activity budgets available. Captive studies may therefore provide baseline behavioral data for researchers in the wild to compare against, or in captivity to test enrichment effects. Second, the study may be used to trial the use of nocturnal camera technology to determine its effectiveness on a nocturnal bird species.

Materials and methods

Study subjects and locations

Observations were conducted from 19 July to 20 October 2019, at Paradise Park, Hayle, and Cotswold Wildlife Park and Gardens, Burford, both of which are located in the United Kingdom. Three groups of *P. strigoides* were observed during the study: these consisted of a mixed-sex hand reared group, a pair, and a pair with their most recent offspring (Table 1). All individuals were maintained in outdoor aviaries. At Cotswold Wildlife Park, birds were fed at 16:00 daily, whereas at Paradise Park the birds were fed between 15:00 and 16:00. Meals varied on a daily basis, but common food items for both consisted of mealworms (*Tenebrio molitor*), desert locusts (*Schistocerca gregaria)*, and defrosted mice. Paradise Park was open to visitors from 09:00 until 18:00, and Cotswold Wildlife Park was open from 10:00 until 18:00. The birds were therefore visible to the public during these periods. No changes were made to the normal husbandry routines during the data collection period.

Data collection

Prior to data collection, approval was granted by the ethical panels at University Centre Sparsholt, Cotswold Wildlife Park and Paradise Park respectively. Observations were conducted using an Amyway 10000mAh Spy Camera Power Bank (ASIN: B07TFHLJDD), which was able to record behavior during both the day and the night. The camera used infra-red light in order to take footage of the animals during dark, so did not create flashes and should not have disturbed the birds. It was positioned so that it had coverage of most of the exhibit, and in a position that did not obstruct the movements of the birds. Each group of birds was observed for 30 hours each, resulting in 90 hours of observations in total. Observations were conducted during both the day and night, with all observations separated

from each other by at least one hour to avoid pseudo-replication.

An ethogram was developed and trialed on the birds during a two-hour pilot study. Behaviors were originally selected using prior research on *P. strigoides* by Kaplan, [6,8] (Table 2,3). The ethogram was further refined following the pilot study, with behaviors that were not observed being removed. The birds were observed using instantaneous scan sampling at one-minute intervals for one-hour observation periods [24]. Scan sampling was selected as the behavioral recording technique as the birds could not always be reliably identified from one another. Additionally, continuous scan recording for selected event behaviors was conducted for all groups (Table 3).

In addition to behavior, weather conditions were recorded in order to evaluate their effects on behavior. The measured effects included time of day (day or night, based on sunset and sunrise times), temperature and humidity: these were recorded from World Weather online [25]. https://www.worldweatheronline.com/ using the closest locations to each collection.

Data analysis

The behaviors were recorded in a Microsoft Excel™ 365 spreadsheet, and uploaded to Minitab, version 19 for analysis. Activity budgets were generated to compare night and day activity across the three different groups. General Linear Mixed Models (GLMM) were used to determine the effects of the predictors of time of day and group on *P. strigoides* state behaviors. The temperature and humidity were included as random factors in the model. The GLMMs were run on a transformed data set (each hour of data was divided by the number of frogmouths in the group), so that all data were comparable.

Results

A graph was generated to show the differences in the prevalence of state behaviors between the different *P. strigoides* social groupings, and between day and night (Figure 1). Behavioral prevalence is shown as an activity budget to account for differences in social group size. There were considerable differences in behavioral repertoire between day and night observations, with behaviors such as roosting occurring more often during the day, and head bobbing and upright observing occurring more frequently at night. Differences in behavioral prevalence were identified between social groups: observing in an upright stance, for example, was more prevalent in the pair than the trio or the group of five. However, these inter-group differences were much smaller than the differences between day and night. The rate of occurrence of event behaviors was also illustrated using a comparative graph (Figure 2).

Overall, the activity budget revealed that several behavior types were observed more or less frequently between day and night. The five behaviors: head bobbing, huddling, roosting, observing skyward and observing slouched were selected for further investigation. GLMMs were run on all five tests, revealing significant effects of time of day in all cases. Group was also a predictor of changes in head bobbing and observing upright, and humidity was a predictor of changes in head bobbing, observing upright and observing slouched (Table 3). The tests were able to explain between 46% and 90% of the observed variation in behavior. Temperature appeared to have minimal impact on the behavior of the *P. strigoides* in the study.

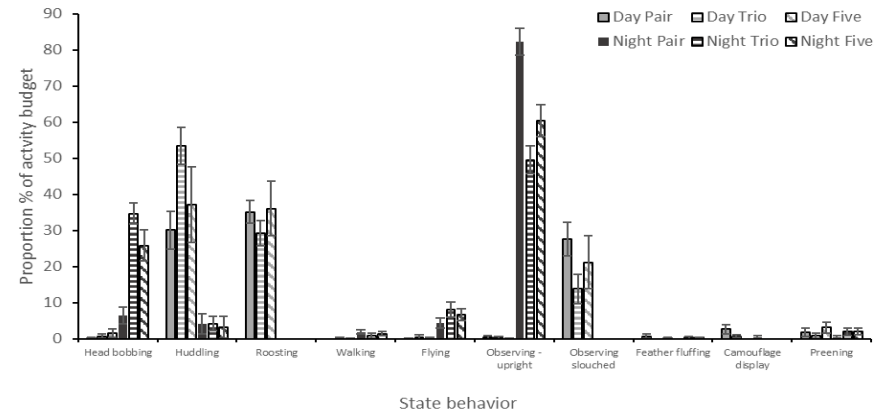

Figure 1: Tawny frogmouth activity budget (± standard error).

Figure 2: Tawny frogmouth activity budget (± standard error).

Table 1: Study subjects

Location	Group (number of birds)	ID	Gender	Age at time of study	Rearing method
Cotswold Wildlife Park	Pair and youngest offspring (3)	BB891	Male	12 May 2007	All parent reared
		BB5980	Female	11 Jul 2004	
		BB3639	Male	5 May 2019	
Cotswold Wildlife Park	Pair (2)	BB3716	Male	26 Jul 2012	Both parent reared
		BB3379	Female	14 Jun 2017	
Paradise Park	Mixed sex (5)	B445	Male	5 Apr 2016	All hand reared
		B460	Male	29 Jun 2017	
		B461	Male	3 Jul 2017	
		B465	Female	16 May 2018	
		B466	Female	17 May 2018	

Table 2: Ethogram of state behaviors. Developed and adapted from works by Kaplan [6,18].

Behaviour	Description
Camouflage display	Eyes are closed, wings tucked, head raised, and body is elongated
Feather fluffing	Feathered are fluffed, especially along top of back and wings, designed to make bird appear bigger and threatening, aggressive behaviour
Flying	The bird beats its wings to travel through the air.
Head bobbing	The head moves up and down several time whilst the body remains motionless.
Huddling	Two or more frogmouths sit in close proximity with eyes partially or fully closed.
Observing upright	Head tilted upwards to allow observation of the sky. Eyes are open and body may be motionless or with head moving.
Observing slouched	Bird is perching, eyes wide open, movement of head to watch surroundings.
Preening	Beak is used to groom feathers.
Roosting	Eyes are partially or fully closed whilst perching on a branch
Walking	The bird moves using its feet.

Table 3: Ethogram of event behaviors. Developed and adapted from works by Kaplan [6,18].

Name of behavior	Description
Beak wiping	The bird rubs its beak against a branch or solid object
Body fluffing	The feathers of the body are erect for a short time before shaking the body to revert feathers to original state
Scratching	The head and/or neck are swiped using the foot
Stretching	The extension of the wings and/or legs for longer than one second

Table 4: Outputs from GLMs on selected tawny frogmouth behaviors.

Behaviour	Adjusted r-squared	Condition	Coefficient	F-value	P
Head bobbing	66.23%	Time of day	-9.91	79.07	<0.001
		Group	-5.79 (2), -2.34 (5)	15.76	<0.001
		Temperature	0.781	0.69	0.407
		Humidity	0.892	6.37	0.014
Huddling	56.39%	Time of day	16	58.39	<0.001
		Group	-4.78 (2), 1.16 (5)	1.14	0.324
		Temperature	0.31	0.03	0.869
		Humidity	-1.614	5.91	0.017
Roosting	69.42%	Time of day	17	150.33	<0.001
		Group	0.79 (2), 1 (5)	0.46	0.634
		Temperature	-0.05	0	0.968
		Humidity	0.179	0.17	0.685

Observing upright	90.34%	Time of day	-32.97	603.01	<0.001
		Group	7.63 (2), 1.65 (5)	14.7	<0.001
		Temperature	-0.43	0.15	0.701
		Humidity	-0.94	4.87	0.03
Observing slouched	46.64%	Time of day	12.02	67.75	<0.001
		Group	2.77 (2), -1.36 (5)	0.5	0.61
		Temperature	-0.4	0.11	0.744
		Humidity	1.105	5.69	0.019

Discussion

Overall, *P. strigoides* showed major differences in behavior between the night and the day, with the majority of active behaviors occurring at night. This suggests that as with wild birds, *P. strigoides* are less active in the day in captivity, as in the wild [8]. Social grouping also appeared to have an impact on *P. strigoides* behavior, with group size playing a significant effect on the behaviors of observing, slouched and upright postures, and head bobbing. Both temperature and humidity, by contrast, appeared to have minimal effects on the behaviors expressed by the birds.

Tawny frogmouth behavior

Observations during the day showed mostly inactive behaviors from the *P. strigoides*, irrespective of social grouping. This seems to match wild research, which shows that *P. strigoides* often sit in positions that make the best use of their camouflage throughout the day [6,12]. For the purpose of this study, we separated out some of the inactive behaviors seen in *P. strigoides*, as some of the behaviors appear to play different biological roles. For example, observing in the slouched posture seems to have some camouflage value, as this posture allows *P. strigoides* to mimic a broken branch on many *Eucalyptus spp.* trees [7,26]. By contrast, huddling is more closely associated with maintaining body temperature [3]. It is interesting to note that the trio and group of five were the two groups which huddled most frequently, and also were the groups that contained juvenile birds. It is possible that huddling may be more important as a thermoregulatory strategy for juvenile, rather than adult birds [10,11]. In the wild, *P. strigoides* is known to sometimes enter a state of torpor during the day [3,9]. This torpor is believed to be an additional energy saving strategy, in order to balance energy budgets which are constricted by low calorie insect-based diets. Similar strategies are utilized by insectivores in other taxa. For example, the giant anteater (*Myrmecophaga tridactyla)* has a reduced metabolic rate than would be expected for a mammal of equivalent size [27]. Thermoregulatory strategies, either as huddling for warmth or positioning to reduce heat loss during the day, may be important behaviors for both wild and captive individuals [12].

Wild frogmouths have been recorded sitting in positions that optimize their ability to mimic their surroundings: the birds often select roosts that are similar in color to their feathers [3]. The slouched posture is believed to be a camouflage response, to protect inactive individuals against predation. It appears that this behavior seems to occur even in captivity.

The cameras used for this study were able to record data continuously. By contrast, many cameras used for wildlife study are triggered by motion: this might result in inactive or subtle behaviors being underestimated. To develop this study further, comparative wild data could be generated by setting up cameras near to favored *P. strigoides* roosts.

Social grouping

Three different social groupings of birds were included in the study: these consisted of a pair, trio and group of five individuals. There were also differences in terms of rearing method, in that the group of five birds were hand reared, whereas all other birds were parent reared. This difference in social grouping is likely to have presented the study with variation in behavior.

However, while significant differences in behavior were attributed to social grouping, this was only for two behaviors studied (head bobbing and observing postures). In comparison, time of day was identified as having a much greater influence on behavior. This indicates that while social grouping and rearing methods clearly do have an impact on behavior, all groups still changed their behavior between day and night in a predictable way. This suggests there may be some external validity to the findings.

Four event behaviors were identified during the study: these were scratching, beak wiping, body fluffing and stretching. Whilst statistical analyses were not conducted on these behaviors given their relative rarity, it is interesting to note that the prevalence of events was similar for both day and night behavioral observations. The prevalence of events seemed to be related more to the social grouping of birds rather than the time of day: For example, the pair of frogmouths were observed engaging in bouts of body fluffing more often, whereas the group of five birds were seen to engage in beak wiping more frequently. These findings differ from those found for state behaviors, in which time of day appeared to be the biggest predictor of behavior change. Events in this study might therefore represent characteristics of individual birds.

Zoo nocturnal studies

The study of nocturnal behavior in the zoo setting is a developing field of study (20,19;16), with some often surprising results with regards to nocturnal activity for species that are typically considered to be diurnal. By contrast, it is perhaps unsurprising that *P. strigoides* are more active at night. However, the behaviors identified are particularly unusual: The high prevalence of head bobbing behavior during the night is an example. The value of the study is therefore not be in identifying that in captivity *P. strigoides* is nocturnal, but rather in identifying the behavior of the species at night.

Anecdotally, the researchers identified that zoo visitor knowledge of *P. strigoides* in the United Kingdom is often poor. When preparing for observations, visitors were often overheard describing the frogmouths as owls, or ignoring the exhibit entirely. While both taxa are similar in terms of their anatomical traits, this misunderstanding may limit the educational value of frogmouths in zoos, particularly if visitors are not engaging with educational signage. Moss and Esson [22] identified that

specific traits predicted visitor interest in zoo animals: Of note, these included large body size, active behavior, mammalian taxa, and being the focus of an exhibit. As a medium-sized nocturnal, dark-colored bird, frogmouths do not have much visitor holding power.

Novel housing styles and use of technology could be used to enhance visitor interest in frogmouths by showcasing the species' diverse nocturnal behaviors. For example, nocturnal houses have been built in many zoological collections, using a reverse light cycle to show animals during their active periods [17]. Frogmouths could be an interesting addition to these houses, encouraging collections to keep a more diverse array of nocturnal species [18]. Similarly, inclusion of the frogmouth into zoos that offer controlled night-time events such as a Night Safari, or by making available recorded night footage may be good ways of engaging with the public.

In terms of feeding, the birds studied were not observed eating during the study. However, feed was normally provided during the day as part of the normal husbandry routine, and observations were not undertaken when keepers were present in the exhibit. While there is limited research on the nocturnal behavior of frogmouths either in the wild or in captivity, it has been suggested that *P. strigoides* are adept hunters of insects, and use strategies such as hawking to capture flying prey [8]. Foraging for invertebrates such as moths is likely therefore to occur more frequently during the night for wild frogmouths, in addition to occasional capture of vertebrates such as rodents [7,28]. The study subjects showed little evidence of foraging behavior during observations. However, flights were observed more frequently during the night observations. One potential enrichment opportunity is to provide a well-shielded light to attract moths into the enclosure and further encourage flight.

Conclusions

Overall, captive tawny frogmouths were most active during the night than the day, showing a totally different behavioral repertoire during hours of darkness. Roosting, head bobbing, huddling and postural changes all differed significantly based on the time of day. Whilst comparatively smaller than the day-night differences, significant differences in behavior were also noted between the pair, trio and group of five birds.

Zoo visitors and researchers alike are most likely to observe the tawny frogmouth during its period of inactivity during the day. This might result in the species being labelled as inactive or sedentary. By contrast, this study revealed unusual nocturnal behaviors such as head bobbing, and a much greater frequency of flight during the night. Further study, focusing on wild individuals, could help to develop comparisons between wild and captive birds. Use of nocturnal, continuous recording cameras placed strategically by preferred perching may help to further advance current knowledge of frogmouth behavior and nutrition.

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