Comparing behaviour of wild and captive flamingos: An evaluation of published data on time-activity budgets

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Abstract

Flamingos have become popular subjects for behavioural studies, both in the wild and in captivity. Improving animal welfare in captivity underpins conservation outcomes, and one of the ways of benchmarking "good welfare" is to understand a species' wild behaviour patterns. Research on wild flamingo time-activity budgets helps develop welfare assessments for captive flocks, and captive studies allow researchers to collect long-term data on individual birds. In order to provide such a benchmark for behavioural scientists with an interest in flamingo behaviour, conservation and welfare, we collated published papers containing the activity budgets of wild and captive birds of all six flamingo species. Overall, some variation in the time-activity budgets calculated for flamingos was noted, which is likely to be a result of different flock demographic and physiological state, environmental conditions, habitat and location, and time of observations. However, several key behaviours, namely feeding (walk-feeding and stamp-feeding), resting and preening take up a considerable portion of both wild and captive flamingo activity budgets. There were few inconsistencies between the behaviours of wild and captive flocks, suggesting that captive birds may have the opportunity in zoos to express most of their natural behaviours. Resting was increased and foraging decreased in captive compared to wild flocks, which may be caused by husbandry protocols. Future attention should be paid to the timings of observations, so that research captures a full 24-hour time-activity budget, rather than just focussing on diurnal behaviour patterns.

Resumen

Los flamencos se han convertido en sujetos populares para estudios de comportamiento, tanto en silvestría como en cautiverio. Mejorar el bienestar animal en cautiverio es la base de los resultados de conservación, y una de las formas de comparar el "buen bienestar" es comprender los patrones de comportamiento de la especie en su hábitat natural. La investigación sobre los presupuestos de actividad de tiempo de los flamencos silvestres ayuda a desarrollar evaluaciones de bienestar para los grupos en cautiverio, y los estudios en cautiverio permiten a los investigadores recopilar datos a largo plazo sobre aves individuales. Para proporcionar un punto de referencia para los científicos interesados en el comportamiento, la conservación y el bienestar de los flamencos, recopilamos documentos publicados que contienen los presupuestos de actividad de las seis especies de flamencos en silvestría y cautiverio. En general, se observó cierta variación en los presupuestos de actividad temporal calculados para los flamencos, que probablemente sea el resultado de diferentes estados demográficos y fisiológicos, condiciones ambientales, hábitat y ubicación, y tiempo de observación de la parvada. Sin embargo, varios comportamientos clave, como la alimentación (alimentación caminando y alimentación

con zapateo), descanso y acicalamiento ocupan una parte considerable de los presupuestos de actividad de ambos tipos de flamenco. Hubo pocas inconsistencias entre los comportamientos de las bandadas silvestres y en cautiverio, lo que sugiere que las aves en cautiverio pueden tener la oportunidad en los zoológicos de expresar la mayoría de sus comportamientos naturales. El descanso se incrementó y la alimentación disminuyó en cautiverio en comparación con las bandadas silvestres, lo que puede ser causado por los protocolos de manejo. A futuro se debe prestar atención a los horarios de las observaciones, de modo que la investigación capture un presupuesto de actividad de tiempo completo de 24 horas, en lugar de centrarse solo en los patrones de comportamiento diurno.

Résumé

Les flamants roses sont devenus des sujets populaires d'études comportementales, à la fois dans la nature et en captivité. L'amélioration du bien-être des animaux en captivité conditionne les résultats en matière de conservation, et l'un des moyens de mesurer le «bien-être» consiste à comprendre les comportements sauvages de l'espèce. La recherche sur les budgets temps-activité du flamant sauvage aide à développer des évaluations du bien-être des groupes en captivité, et des études en captivité permettent aux chercheurs de collecter des données individuelles à long terme. Afin de fournir un tel point de repère aux scientifiques s'intéressant au comportement, à la conservation et au bien-être des flamants, nous avons rassemblé des articles publiés contenant les budgets d'activité des oiseaux sauvages et captifs des six espèces de flamants. Globalement, une certaine variation dans les budgets temps-activité calculés pour les flamants a été observée, ce qui est probablement dû à différents états démographiques et physiologiques des oiseaux, aux conditions environnementales, à l'habitat et à l'emplacement, ainsi qu'à l'heure des observations. Cependant, plusieurs comportements clés, à savoir l'alimentation (alimentation à la marche et au piétinement), le repos et le toilettage, absorbent une part considérable du budget d'activités des flamants sauvages et captifs. Il y avait peu d'incohérences entre les comportements des groupes d'oiseaux sauvages et captifs, ce qui suggère que les oiseaux captifs ont la possibilité d'exprimer la plupart de leurs comportements naturels dans les zoos. Le repos était augmenté et la recherche de nourriture diminuée chez les captifs par rapport aux groupes sauvages, ce qui peut résultédes protocoles d'élevage. À l'avenir, il faudra accorder une attention particulière au moment choisi pour les observations, afin que la recherche puisse établir un budget temps-activité de 24 heures, au lieu de se concentrer uniquement sur les schémas comportementaux diurnes.

Introduction

The behavioural performance of captive flamingos can be restricted by the confines of the zoo environment (e.g. enclosure size) and by management practice (e.g. flight restraint) or the logistics of building an exhibit (e.g. aviary style and height). Data collection on the time-activity budgets of captive flamingos can provide useful details on how birds interact with their environment and how they experience positive welfare states- based on the performance of a naturalistic time budget.

The study of animal behaviour provides insight into the ecology of wild species and their evolutionary characteristics that are relevant to developing and evaluating captive management protocols. To develop best practice husbandry and encourage breeding in captive collections, wild animal time-activity budgets are often used as a benchmark (Brereton et al., 2018; Howell & Cheyne, 2018). Social (e.g. flock size) and environmental factors (e.g. style of exhibit) can play a role in determining the time-activity

budgets performed by captive flamingos (Greene & King, 2005; King, 2008; Rose et al., 2018a).

Therefore, comparing data on the activity of wild flocks to those housed in captivity is a useful way of i) assessing "behavioural normality" and ii) providing evidence for the good quality care (i.e. if activity patterns are similar, husbandry protocols are likely to be relevant). The activity budgets of wild flocks may be used to determine whether zoo-housed flocks have the opportunity to display the same behavioural diversity recorded for *in situ* flocks. Activity budgets may also be highly valuable for assessing the behavioural effects of changes to exhibit design and husbandry protocols, as well as influences of season or flock size.

Flamingo behaviour

The six extant species of flamingo have received considerable research attention from both ecologists (Arengo & Baldassarre, 2002; Naz et al., 2018) and zoo biologists (Pickering et al., 1992; Rose et al., 2014; Stevens & Pickett, 1994). Individual birds can be easily identified using physical characteristics or leg rings (Rose & Croft, 2015, 2017) and the birds are sufficiently long lived to allow for long-term studies (Stevens & Pickett, 1994). The gregarious nature of the flamingo also aids researchers in overcoming the sample size issue that is commonly associated with ecological and zoo studies (Rose et al., 2018b). Wild flocks may be in excess of thousands of birds (del Hoyo, 1992), and even captive flocks may reach over 100 individuals in size (Rose & Croft, 2018), providing a valid tool for the study of behaviour in a species whose wild movement patterns may make it tricky to follow.

Given their suitability for scientific study, flamingos have been the focus of a range of research topics including laterality, social networks, foraging ecology and breeding behaviour (Amat et al., 2011; Bouchard & Anderson, 2011; Gihwala et al., 2017; Hughes et al., 2013). And range of behavioural studies have been conducted that illustrate the time-activity budgets and behaviour patterns of both wild and captive flocks, with some papers attempting a direct comparison of wild and captive behavioural repertoires. (Bildstein et al., 1991; Bildstein et al., 1993; Derlindati et al., 2014).

Wild flamingos show considerable behavioural diversity and use multiple feeding and foraging methods (Boukhriss et al., 2007b; Espino-Barros & Baldassarre, 1989; Robinson, 2015). Flamingos also show a wide range of reproductive behaviours, exhibiting stereotyped display behaviours that may be performed by an individual or across the whole flock (Bouaguel et al., 2013; Perrot et al., 2016). Vigilance behaviour also comprises a significant proportion of wild flamingo time-activity budgets as an anti-predatory mechanism (Beauchamp, 2006; Beauchamp & McNeil, 2003, 2004; Boukhriss et al., 2007a; Boukhriss et al., 2007b; Galicia & Baldassarre, 1997). Consequently, data on key state behaviours, which fill a large part of a wild flamingo's time, are freely available in the literature to use for captive bird comparative studies.

Considering diurnal and nocturnal flamingo behaviour

Many waterfowl species show nocturnal behaviour in some parts of their native ranges (McNeil et al., 1992; McNeil et al., 1993) and flamingos are similar in this respect (Boukhriss et al., 2007a; Tindle et al., 2014). Birds may choose to feed at night in order to avoid the attention of predators in their local area, spending long periods during evening and overnight engaged in foraging behaviour (Rendón-Martos et al., 2000). Previous research on wild greater flamingos (*Phoenicopterus roseus)* in France and Spain has demonstrated that these birds may engage in a range of feeding and vigilance activities throughout the night (Beauchamp & McNeil, 2003; Britton et al., 1986; Rendón-Martos et al., 2000). Diurnal studies on captive

flamingos have shown differing results. Some populations of flamingos appear to spend large portions of the day being active (Arengo & Baldassarre, 2002; Schmitz & Baldassarre, 1992), whereas other authors cite relatively low overall activity (Bildstein et al., 1991). Activity levels are therefore likely to vary not only based on the time of day, but also as a result of weather conditions, predation risk, food availability and foraging patch quality, bird physiological state (e.g. in and out of the moult), flock demographics and encounters with other species.

In parallel with wild studies, captive flamingo research has also begun to address some of the questions surrounding nocturnality. Research on a captive flock of greater flamingos showed activity throughout the night, with flamingos making considerable use of water features in their exhibit (Rose et al., 2018b). It is likely that many captive flamingo flocks show similar time-activity budgets: Lower activity levels around midday and a much higher degree of activity in morning and evening. However, as the majority of captive studies focus on flamingo behaviour during typical zoo opening hours, understanding of their complete behavioural repertoire may still be lacking (Rose et al., 2016).

Bridging the gap between wild and captive research

The research interest in both wild and captive flamingos has generated a wealth of literature, however, the behaviour of flamingos *in situ* and *ex situ* is not always compared. Comparison of activity budgets can provide keepers with the information needed for the implementation of evidence-based husbandry measures to ensure their flamingos can engage in the same diversity of behaviours seen in wild birds. Data generated from captive studies can be valuable for identifying the activity patterns of individual birds, particularly with a focus on changes in behaviour and social networks over months or years, and therefore provide relevant information on individuality helpful to conservationists working with wild groups.

The IUCN "One Plan Approach" to conservation states that both wild and captive individuals should be considered as one population (CBSG, 2015). One Plan aims to facilitate the transfer of genetics and information between wild and captive populations (Conde et al., 2013). Given that four of the six extant flamingo species are considered to be of conservation concern, closer alignment of wild and captive behavioural research can help underpin successful conservation outcomes for flamingos.

Consequently, the aim of this study was to identify the normal time-activity budgets of wild flamingos of all species, based on the published literature. The study also aimed to consolidate the existing literature on captive flamingo time-activity budgets to identify differences in behaviour patterns between species or between wild and zoo-housed flocks. This comparison of time-activity budgets may help identify aspects of husbandry that keepers can develop to enable captive flamingos to act like their wild counterparts and promote positive welfare states.

Methods

We conducted a review of the existing literature on flamingo behaviour. In order to identify relevant papers, we searched the Web of Science© and Google Scholar journal databases, using any combination of the terms flamingo, *Phoenicopterus* or *Phoenicoparrus*, and activity budget, activity pattern, behaviour or behavior. Studies on both wild and captive flamingos were included within the dataset. Papers were scrutinised from 1970 to 2019. Papers were excluded if they did not provide information on behavioural observations or time-activity budgets of flamingos.

For each paper identified, the flamingo species, location and its presence in the wild

or in captivity was noted. Additionally, the observed behaviours and the amount of time spent engaged in the behaviour was noted. Using all the behavioural data identified, the average time-activity budget for a wild and for a captive flamingo was calculated using generic behavioural categories (such as active, inactive and feeding). All data are summarised in Table 1. From each research publication collected, the average of key state behaviours (feeding, inactive, flight, courtship, aggression, preening, walking, vigilance and incubation) was calculated for a wild and a captive flamingo.

Results

A total of 22 papers were collected, providing information on activity patterns for all six flamingo species (Table 1). Behavioural data covered both wild and captive flamingo flocks, though information on wild flamingo time-activity budgets was more common. Of all species, the greater flamingo and Caribbean flamingo (*Phoenicopterus ruber)* were the best represented, with the lesser flamingo (*Phoenicoparrus minor)*, puna/James's flamingo (*Phoenicoparrus jamesi)* and Chilean flamingo (*Phoenicopterus chilensis)* being the least often studied. Results show that wild flamingos spend more time on feeding and foraging behaviours, are more vigilance and spend less time on inactivity (Figure 1). Captive birds are less vigilant and spend more time on preening and inactivity (i.e. loafing and resting). Rates of walking are similar between the average captive flamingo and the average wild flamingo, however this rate of walking may increase for wild birds when walk and stamp-feeding is removed from feeding behaviours and included as locomotion. Variation is noted within a species, dependent on location, for time spent feeding. Data from Robinson (2015) for lesser flamingos foraging in East African soda lakes (Table 1) ranges from 46% to 91% of a bird's time budget. Differences in the reasons for inhabiting a specific soda lake (e.g. breeding events or moulting) may account for with within-species variation.

Time allocated to state behaviours also changes at night, with birds spending more time roosting/sleeping during the daytime and then considerably more time spent feeding and foraging overnight.

Table 1: Time-activity budgets for state behaviours of wild and captive flamingos taken from published literature

Author	Year	Journal	Species	System	Location	Observation type	Notes	Behaviour
Britton et al.	1986	Wildfowl	Greater flamingo	Wild	Camargue	Diurnal		Feeding 15%
						Nocturnal		Feeding 85%
Espino-Barros & Baldassarre	1989	Condor	Caribbean flamingo	Wild	Yucatan	Diurnal	Early morning	Feeding 44.3%, Resting 11.5%, Flying 5%, Walking 6.2%, Preening 19%, Courtship 3.3%, Comfort 0.9%, Aggression 2.8%, Alert 1.4%, Nest building 1.5%, Incubation 4.1%
							Late morning	Feeding 33.8%, Resting 20.1%, Flying 3.5%, Walking 6.3%, Preening 20.8%, Courtship 3.2%, Comfort 1.3%, Aggression 2.8%, Alert 1.9%, Nest building 1.4%, Incubation 5%
							Early afternoon	Feeding 32.3%, Resting 18.6%, Flying 3.8%, Walking 7.6%, Preening 21.5%, Courtship 2.7%, Comfort 1.8%, Aggression 3.1%, Alert 2%, Nest building 1.3%, Incubation 5.3%
							Late afternoon	Feeding 35.7%, Resting 10.6%, Flying 6.6%, Walking 9.1%, Preening 21.7%, Courtship 2.8%, Comfort 2.3%, Aggression 3%, Alert 1.7%, Nest building 1.7%, Incubation 4.9%
Bildstein et al.	1991	Condor	Caribbean flamingo	Wild	Cuare National Wildlife Refuge Venezuala	Diurnal		Walking 10%, Walk-feeding 29%, Stamp-feeding 15%, Inactive 38%, Preen 9%
Schmitz & Baldassarre	1992	Condor	Caribbean flamingo	Wild	Yucatan	Diurnal		Feeding (head down) 59%, Resting 0.1%, Walking 3.2%, Preening 3.2%, Feeding (head up) 29.3%, Vigilance 2.1%, Aggression 2.3%
Arengo & Baldassarre	1995	Condor	Caribbean flamingo	Wild	Yucatan	Diurnal		Walk-feeding 75%, Stamp-feeding 25%
Galicia & Baldassarre	1997	Conservation Biology	Caribbean flamingo	Wild	Yucatan	Diurnal		Stamp-feeding 31%, Resting 12%, Standing 10%, Alert 2%, Walk-feeding 10%, Walking 7%

Author	Year	Journal	Species	System	Location	Observation type	Notes	Behaviour
Herrera-Silveira & Zaldivar-Jimknez	2001	Yucatán a Través de Los Siglos	Caribbean flamingo	Wild	Yucatan	Diurnal		Feeding 16-65%, Preening 2-9%, Alert 1-24%, Locomotion 17-24%
Arengo & Baldassarre	2002	Condor	Caribbean flamingo	Wild	Yucatan	Diurnal		Walk-feeding 7-73%, Stamp-feeding 14-67%
Derlindati	2008	Rufford Maurice Lang Foundation	Andean flamingo	Wild	Vilama	Diurnal		Resting 7%, Feeding 91%, Vigilance 1%, Other 1%
			James's flamingo					Resting 3%, Feeding 91%, Vigilance 6%, Other 0%
			Andean flamingo	Wild	Melincue	Diurnal		Resting 32%, Feeding 57%, Vigilance 1%, Other 10%
Mawhinney	2008	Physis	Caribbean flamingo	Wild	Antilles	Diurnal		“Grubbing” 39%, Skimming 24%, Seizing 17%, Stabbing 9%, Searching 8%, Walking 2%
Bouaguel et al.	2013	Annals of Biological Research	Greater flamingo	Wild	Algeria	Diurnal	Winter morning	Resting 3.04%, Preening 6.25%, Feeding 70.71%, Locomotion 17.96%, Flight 2.08%, Courtship 0.96%,
							Winter afternoon	Resting 0.33%, Preening 3.5%, Feeding 73.67%, Locomotion 9.75%, Flight 11.04%, Courtship 1.71%,
							Summer morning	Resting 1.67%, Preening 4%, Feeding 74.92%, Locomotion 15.75%, Flight 1.29%, Courtship 2.38%,
							Summer afternoon	Resting 0%, Preening 2.21%, Feeding 74.54%, Locomotion 5.83%, Flight 6.29%, Courtship 4.25%,
Derlindati et al.	2014	Ornitologia Neotropical	Andean flamingo	Wild	Laguna de Vilama and Laguna Melincue	Diurnal		Preening 21%, Walk-feeding 73%, Stamp-feeding 4%
					Laguna Melincue			Preening 19%, Stamp-feeding 31%, Walk-feeding 20%, Resting 14%, Walking 7%

Author	Year	Journal	Species	System	Location	Observation type	Notes	Behaviour
Kumssa & Bekele	2014	International Journal of Biodiversity	Lesser flamingo	Wild	Ethiopia	Diurnal		Feeding 68%, Moving 6%, Resting 9%, Preening 10%, Vigilance 6%
Robinson	2015	Thesis	Lesser flamingo	Wild	Bogoria North	Diurnal		Feeding 46%
					Bogoria Central			Feeding 67%
					Bogoria South			Feeding 42%
					Nakuru Njoro River			Feeding 68%
					Nakuru Lake			Feeding 74%
					Elementaita			Feeding 91%
					Oloiden Public			Feeding 60%
					Sonachi			Feeding 76%
					Natron South			Feeding 78%
Bensaci et al.	2015	International Journal of Biological, Biomolecular, Agricultural, Food and Biotechnological Engineering	Greater flamingo	Wild	Algeria	Diurnal	Oued Righ Valley	Feeding 66.29%, Sleeping 10.79%, Flying 2.31%, Walking 6.19%, Courtship 2.52%, Aggression 2.81%, Preening 4.89%,
							Central Hauts Plateau	Feeding 69.09%, Sleeping 8.22%, Flying 2.06%, Walking 12.28%, Courtship 1.73%, Aggression 2.48%, Preening 4.12%,
Naz et al.	2017	Environmental Science and Pollution Research	Greater flamingo	Wild	Uchalli Lake, Punjab	Diurnal		Feeding 51%, Resting 10.9%, Flight 10%, Walking 10.9%, Preening 3.6%, Aggression 2.6%, Alert 8.3%
Boukhriss et al.	2007	Ostrich	Greater flamingo	Wild	Gulf of Gabés	Diurnal		Feeding 20%, Sleeping 30%, Cleaning 15%, Vigilance 20%
Boukhriss et al.	2007	Ethology	Greater flamingo	Wild	Gulf of Gabés	Nocturnal		Feeding 45%, Vigilance 16%, Looking for food 2%, Preening 9%, Roosting 18%

Author	Year	Journal	Species	System	Location	Observation type	Notes	Behaviour
O'Connell-Rodwell & Rodwell	2004	Bird Conservation International	Caribbean flamingo	Captive	Guana island	Diurnal		Feeding 55-68%, Resting 15-27%, Preening 8-11%, Head-flagging 1.8%, Reproductive 1.8%
George et al.	2013	Bristol Zoo Poster	Greater flamingo	Captive	Bristol Zoo Gardens	Diurnal		Active 48%, Inactive 33%, Breeding 3%, Aggressive 1%
Finlay et al.	2017	Dissertation	Caribbean flamingo	Captive	Zoo de Granby	Diurnal	Morning	Resting 16%, Preening 11%, Foraging 8%, Locomotion 3%, Vigilance 1%
							Afternoon	Resting 13%, Preening 12%, Foraging 10%, Locomotion 3%, Vigilance 1%
Brereton et al.	2018	Flamingo	Greater flamingo	Captive	ZSL London Zoo	Diurnal	Breeding	Loafing 32%, Incubating 16%, Resting 24%, Vigilance 2%, Preening 8%, Locomotion 4%, Foraging 8%, Aggression 1%, Display 1%
Rose et al.	2018	Applied Animal Behaviour Science	Greater flamingo	Captive	WWT Slimbridge	Diurnal		Active 48%, Inactive 52%
			Caribbean flamingo					Active 52%, Inactive 48%
			Chilean flamingo					Active 43%, Inactive 57%
			Andean flamingo					Active 45%, Inactive 55%
			Lesser flamingo					Active 41%, Inactive 59%
Rose et al.	2018	Zoo Biology	Greater flamingo	Captive	WWT Slimbridge	Diurnal		Inactive 30%, Locomotion 36%, Foraging 29%, Display/Nest 5%
						Nocturnal		Inactive 33%, Locomotion 36%, Foraging 28%, Display/Nest 3%

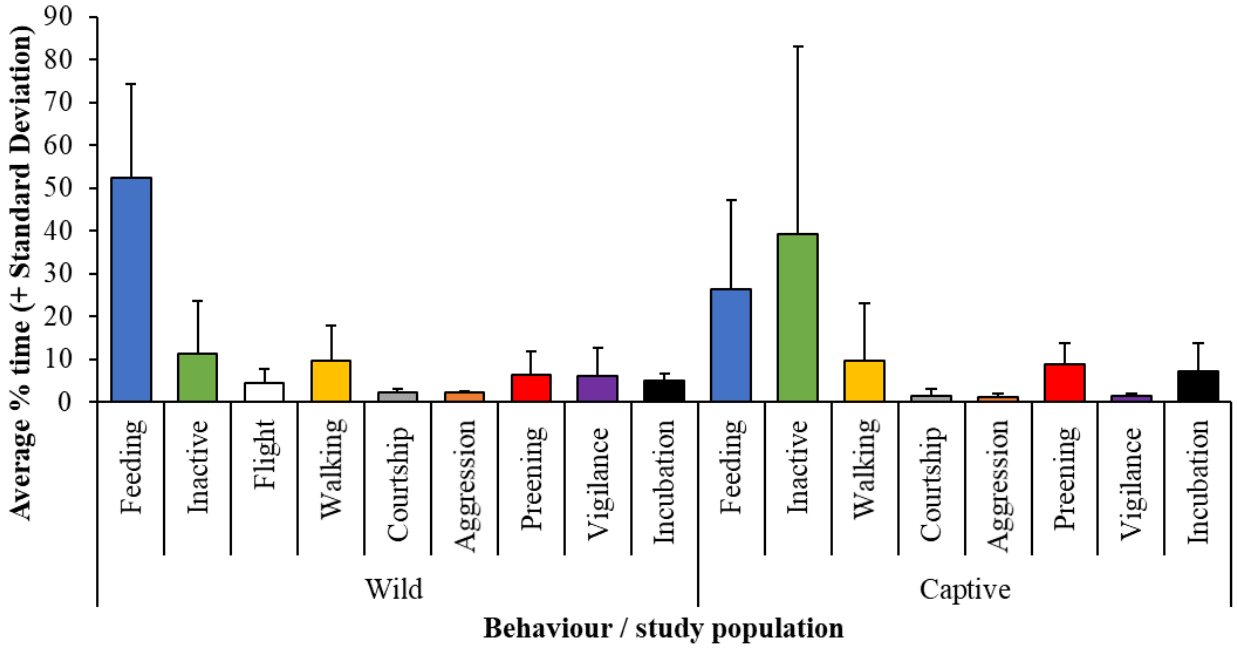

Figure 1: A comparison of the time-activity budget of a wild flamingo compared to a captive flamingo using data averaged (+ standard deviation) from the information presented in Table 1.

Discussion

Interpreting activity budgets

Across flamingo species, several behaviours appeared to stand out regarding their frequency of occurrence in published work: Resting, locomotion and preening often featured in activity budgets (though specific times were variable). Feeding behaviours were very well represented, and two forms (stamp feeding and walk feeding) were a regular feature for both wild and captive individuals. Vigilance /alertness also appeared on most flamingo activity budgets, although again the actual amount of time varied between studies.

There was great variation in the representation of key state behaviours per paper. Feeding and foraging ranged between 20% and 100% of selected time-activity budgets. This variation may be attributed to a wide range of methodological, environmental and demographic differences between flocks, in addition to species differences. To investigate this variation further, several studies collected data on multiple flocks for comparison (Bensaci et al., 2015; Derlindati et al., 2014; Rose et al., 2018a). For these studies, the methods were standardised across all flocks, thus reducing the confounding methodological effects. Between flocks of the same species, Derlindati et al. (2014) found differences in feeding strategies employed (stamp-feeding versus walk-feeding). Similarly, Bensaci et al. (2015) identified diversity in the prevalence of aggression and flight in the flocks of greater flamingos studied. Flamingo time-activity budgets are clearly heavily influenced, within species, by the habitat the birds are within.

Even amongst the same flock, the season and time of day appears to have a profound effect on flamingo behaviour. For example, the prevalence of preening, courtship and flight vary considerably with the time of day (Bouaguel et al., 2013); during the spring and summer, prevalence of courtship behaviours dramatically increased, impacting the overall prevalence of resting and preening. Similar findings have been attributed to captive birds: Greater flamingos, studied overnight use different resources (i.e. exhibit areas)

compared to during the day (Rose et al., 2018b). Whilst some researchers included night-time observations in their studies (Beauchamp & McNeil, 2003), a majority of studies covered only diurnal observations. To improve the overall quality and reliability of these behavioural data, researchers should consider observing flamingo behaviour across the full 24-hour cycle, so that the time for the performance of key behaviours is not neglected.

While some of the variation in activity patterns is likely due to methodological differences, these data do suggest that flamingos show a level of behavioural flexibility, allowing them to modify their actions to best suit their current situation. Beauchamp and McNeil (2003) identified that greater flamingos engaged in more bouts of vigilance when they were foraging in smaller flocks and flamingos may change their foraging strategy to best suit their environment (Derlindati et al., 2014). Some species of flamingo (i.e. more generalist feeders) have an ability to adapt to some degree of environmental change, providing that this is within the bird's preferred habitat choice.

Wild versus captive flocks

Overall, there are several key differences in the activity patterns of wild and captive flamingos. Time spent feeding/foraging is considerably lower than those reported for wild birds. This may be a direct result of the captive environment, in which highly-nutritious, high calorific food is provided on a predictable schedule (Rose et al., 2016). This may lead birds to reach their daily energetic requirement more quickly than they would in the wild, resulting in a reduction in foraging time as this is un-needed. Higher levels of inactivity in captive flamingos (Figure 1) may therefore be explained by this too.

Researchers of wild birds may also be focussing on birds when they are foraging, thus leading to inflated values for feeding-related behaviours. Foraging behaviour is a topic of particular interest for researchers of wild flamingos, so timing of observations and observation techniques may be specialised toward this (Mawhinney, 2008). Of particular note, a greater proportion of nocturnal studies have been undertaken in wild, rather than captive flocks, and foraging activity is specifically mentioned in these published works. For example, one paper specifically related flamingo nocturnal activity to the presence of their preferred foodstuff Artemia (Britton et al., 1986). Even in the wild studies that focussed on behaviour in general, high values for feeding behaviour were still recorded. As such, we can reliably say that captive flamingos appear to be spending a lower proportion of their daily time-activity budget engaged in feeding behaviour.

Locomotory behaviour also appears to be considerably lower for captive flocks, with a lower proportion of captive time-activity budgets being spent on this activity. Flight is generally absent in captive flocks, but this is to be expected as flamingos are generally flight restrained in some form. And even when housed in aviaries, it is unlikely that birds will fly in the same way and for the same time as those that are free-living. Wild flamingos generally use flight for travelling between feeding and foraging areas (Krienitz et al., 2016; Parasharya et al., 2015; Pennycuick & Bartholomew, 1973) so quality space for terrestrial behaviours may be more important to them in captive settings. However, this aspect of captive management needs investigation. Currently, there are also limited data to identify whether flight restraint has a large impact on flamingo welfare (George et al., 2013), although some data suggests there may be a negative impact on fertility (King & Bračko, 2014).

Research shows that aggression levels were on, average, higher for wild flocks, suggesting that some aspect of aggression may be a natural part of their social communication. However, the fact that wild flocks appear

more active and the times of year that flamingos were observed (e.g. during the breeding season) may account for this potential increase. It is the context of aggression for captive flamingos that is important (Soole, 2016, 2017), which must be considered if aggression is deemed an indicator of impoverished welfare (Espino-Barros & Baldassarre, 1989).

The prevalence of vigilance was lower in captive flocks on average. In theory, vigilance behaviour may become unnecessary in a captive environment as the presence of predators is much reduced to eliminated. Captive flamingos may also habituate to the presence of human visitors (Rose et al., 2018a), whose presence they cannot avoid, whereas human presence around wild flamingo is noted to cause increases in vigilance and more time being alert (Yosef, 2000). Vigilance is still a feature of time-activity budgets for captive flocks, albeit at a lower prevalence than for wild birds, suggesting that some captive flocks may feel less threatened than their wild conspecifics within the environment provided for them. "Clumping" or tight grouping of flamingos together within an enclosure is a potential indictor of a flock unsettled within its exhibit (King, 2008; Rose et al., 2014), therefore further investigations into the amount of vigilance performed by captive flocks and the context of its performance would provide more information on flamingo welfare states.

Future directions

Currently, there appears to be greater behavioural research output on only a few flamingo species- greater and Caribbean flamingos appear to have received more research attention. These two species are also well-represented in captive collections (King & Bračko, 2014). However, it should be noted that the greater and Caribbean flamingos are both listed as "Least Concern" on the IUCN Red List (BirdLife International, 2016e, 2017). The remaining four species appear as "Near Threatened" or "Vulnerable" (BirdLife International, 2016a, 2016b, 2016c, 2016d), and can breed less reliably in captivity (King & Bračko, 2014; Rose, 2018). To better understand the behavioural ecology of all species, and to provide further evidence for captive care, a greater research focus on the behaviour and activity patterns of lesser, Andean, James' and Chilean flamingos would be helpful.

Many previous studies have also focused in on particular aspects of flamingo behaviour and biology, meaning that researchers select observation times or methodologies that allow them to optimise their investigations of one particular behaviour. To develop a clear understanding of the "normal" time-activity budgets of these birds, research methods should record behaviour across day and night. This would enable the development of time-activity budgets that would be more comparable between flocks or species as a complete picture of the flamingo's 24-hour cycle is provided, helping to drive questions regarding the effects of flock size, sociality or predation risk on flamingo behaviour.

While many aspects of flamingo ecology and behaviour are well studied, several aspects of their biology and husbandry require further focus. For example, triggers of breeding in wild flocks would benefit from further research (Derlindati et al., 2014). Flamingo behaviour is shaped by their intensely gregarious nature, and this evolutionary influence over their time-activity patterns is also worth of further scrutiny. For example, flamingos perform a range of signalling behaviours including head flagging and wing salutes to initiate group courtship display (Studer-Thiersch, 2000). Cooperative foraging strategies, such as stamp-feeding in small groups, can also be observed (Studer-Thiersch, 2000). The influence of number of birds in a captive flock on successful reproductive outcomes is well documented (Pickering et al., 1992); future research should focus on the effects of the social group on these other key state behaviours whose

performance may have important welfare benefits.

Conclusions

Our investigation into the literature has identified variation in the time-activity budgets of wild flamingos. While some of this variation is likely to be a result of differences in study methodology, these findings do highlight the behavioural flexibility of flamingos. We key differences in time spent feeding and being inactive between wild and captive flamingos, with is worthy of further investigation. The variation in data on activity patterns across captive flocks suggests that some captive flamingos may be able to satisfy most of their behavioural needs in a well-designed captive environment. Further nocturnal research would have value in determining whether both populations act similarly across a whole 24-hour cycle. Flamingos are noted to behaviour differently depending on the time of day and they alter behaviour alongside of flock size, environmental parameters, and predation risk. This flexibility may be relevant to the more general flamingo species (greater and Caribbean for example) in identifying and moving into more suitable habitats. Studies of wild birds can provide a benchmark for behaviour patterns that zoo researchers can use when assessing the welfare of their captive flocks. However, not all aspects of wild behaviour can be indicative of good welfare-high vigilance scores, for example, are linked to disturbance or predation risk for wild birds, so the context of wild behaviours used for comparison is key.

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