Applied Animal Behaviour Science 251 (2022) 105626

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim

Evaluation of the time-activity budgets of captive ducks (Anatidae) compared to wild counterparts

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ARTICLE INFO

Keywords:
Behaviour
Wildfowl
Waterfowl
Welfare
Activity
Pinioning
Evidence-based husbandry

ABSTRACT

Ducks are commonly housed in captive environments where their abilities for flight are constrained, either temporarily or permanently. The use of flight restraint in modern animal management is contentious and ethically questioned yet any associated impacts on behaviour remain poorly documented and evaluated. Comparison of information on wild ecology and activity of free-living individuals with information from the same species when captive-housed can reliably inform on "naturalness" of behaviour patterns if standardised methods are used. This research aimed to compare the activity of several species of ducks (Order Anseriformes) with information contained in the literature, and that collected from direct observation, to identify differences between the behaviours of captive and wild ducks. Observational data on the state behaviours for 17 duck species were collected at three Wildfowl & Wetland Trust (WWT) centres in the UK from 2015 to 2018, with behavioural data on two species of wild duck also collected via direct observation. A meta-analysis of time spent on key state behaviours (papers published up until 2018) was performed to provide comparison with the information provided on time-activity budgets of the captive birds. Results showed a multitude of factors influenced captive duck behaviour, but resting, maintenance and locomotion behaviours were most commonly observed. Wild birds differed significantly in their time-activity budgets compared to captive individuals and data from the meta-analysis revealed that foraging rates were higher in the wild than in captivity. Records of abnormal behaviour in captive birds were non-existent to very low in performance, suggesting that flight restrained ducks do not fill part of their time budget with stereotypic behaviour. Human presence may potentially influence of the behaviour of both wild and captive ducks living in wetland areas that attract human visitors. Seasonal, temporal and sex differences significantly also affected wild and captive duck behaviour. Further study should continue to investigate behavioural responses of these species to a range of captive housing to determine the most optimal way of providing for good welfare under human care. Research that investigates the behaviour of fully winged captive ducks to extend our evaluation of behaviour patterns in flight restrained birds (and to provide further review against wild data) is recommended.

1. Introduction

Behavioural measurement is integral to wider evaluation of the suitability of care given to species under human management and associated welfare impacts (Barnett and Hemsworth, 1990; Broom, 1988; Stamp Dawkins, 1989). This care, for many species, can lack an evidence-based rationale and hence poor welfare may occur inadvertently, due to a lack of objective critique of husbandry approaches (Melfi, 2009). Use of ecological data, i.e. information collected from the field on behaviour and adaptations, can be one way of improving and advancing husbandry (Clavadetscher et al., 2021; Fernandez-Duque, 2012), which can lead to the attainment of positive welfare states, i.e. those that are indicative of an animal coping with its environment and experience positive affect and valence (Yeates and

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https://doi.org/10.1016/j.applanim.2022.105626
Received 15 December 2021; Received in revised form 4 April 2022; Accepted 9 April 2022
Available online 13 April 2022

Main, 2008). Birds (Aves) are the most speciose of all taxonomic classes housed in animal collections globally (Rose et al., 2019) and private aviculture also hold substantial populations of bird species too (Rose and O'Brien, 2020). Measuring the behaviour of captive birds can identify differences between wild and captive time-budgets and allow inference of any reasons behind apparent differences (Collias and Collias, 1967; Rose, 2021). For popular species housed under human care certain management techniques (e.g., flight restraint) can be commonly used without consideration of the appropriateness of the technique for the species, its wider impact on the bird's welfare and the ethical consideration of use across all species in a taxonomic group.

Wildfowl (Anseriformes) are a group of around 180 species that comprise the ducks, geese and swans (Anatidae), the magpie goose (Anseranatidae) and screamers (Anhimidae) (del Hoyo et al., 2014; Scott, 1949). Anseriformes are an example of a taxonomic order common to zoos and private collections that are often managed using flight restraint procedures (Krawinkel, 2011; Rose and O'Brien, 2020). Limited work has been performed on the effect of flight restraint on bird behaviour and welfare generally (Schmid et al., 2006), and on Anseriformes specifically, but continued scrutiny over such bird management practices calls for more empirical evidence on the effects of flight restraint to be gathered (Hesterman et al., 2001; Reese et al., 2020). Knowledge of wildfowl ecology may be useful in determining long term beneficial impacts of specific forms of housing, e.g. flight restrained but at liberty compared to fully winged and aviary housed (Rose and O'Brien, 2020). Data on captive behaviour can be compared to published information on the behaviour patterns of free-living individuals to assess where differences in energy partitioning to specific behaviours may occur and why (Rose and Robert, 2013).

All research presented in this paper took place at Wildfowl & Wetlands Trust (WWT) centres in the UK and captive ducks observed for this study were pinioned after hatching, rendering them permanently flightless. All birds were kept in extensive enclosures (all except one enclosure were open-topped) that provided opportunities for swimming and grazing, but increased chances of predation from aerial predators, which is a particular risk when birds are rendered flightless and kept in open pens (Flinchum, 2006). Although flight-associated activities and displays are affected by pinioning, some authorities have documented that other behaviours are unaffected in flight restrained wildfowl (McKinney, 1967). However, flight is beneficial to avian health, providing opportunity for exercise and the prevention of injury (Peng et al., 2013). The restraining of flight may also lead to behavioural abnormalities such as stereotypies (Garner et al., 2003; Peng et al., 2013) and potentially reduce welfare state (Rose and O'Brien, 2020). This can be mediated by the extent of human disturbance on the bird's captive environment (Mason, 1991). Despite these negative effects, captive and/or pinioned birds could still be used to gain insight into wild conspecific behaviour, for example social change associated with breeding activities (McKinney, 1967) or energetic and behavioural changes resulting to different stages or moult (Portugal et al., 2010).

Pinioning is a common flight restriction method used on captive Anseriformes (Antinoff et al., 2002). Long-term physical and psychological effects of pinioning are not yet entirely understood but some authorities state the procedure is painless and stress-free when conducted at a very young age (Flinchum, 2006). Pinioning is a surgical procedure and therefore risks acute pain, haemorrhage and infection, although these are mitigated by appropriate surgical technique, strict asepsis and careful husbandry postoperatively (Hesterman et al., 2001). Chronic pain may be caused if the pinioning site becomes chronically traumatised. The permanent removal of part of the wing also restricts behaviours other than flight, such as courtship displays, and may therefore lead to inadvertent consequences related to other aspects of health (Rose et al., 2014). These can include increased weight gain, time spent standing (leading to an increased risk of developing pododermatitis), reduced muscle and tendon strength (Peng et al., 2013) and potentially frustration, anxiety and physiological stress (Mellor et al., 2018). In some species, research suggest that birds may still be motivated to fly even though they are physically unable to do so (Peng et al., 2013) and therefore the wider behavioural consequences of flight restraint need to be considered on a species-by-species basis (Rose and O'Brien, 2020). Reviewing natural behaviour and ecological specialism may be one way of evaluating responses to flight restraint in captive-housed ducks. Ethically, animal management practices must always consider the ultimate consequences of removing a behavioural trait that a species has evolved to perform, which provides it with functional and adaptive benefits.

Behavioural performance is affected by time of day, species, sex of the bird, and human presence (Baldassarre and Bolen, 1994; Crook et al., 2009; Rose et al., 2020). Other factors influencing activity include body size (i.e. metabolic demand/rate), predation, competition, social status and body condition (Aberkane et al., 2014; Adams et al., 2000; Baldassarre and Bolen, 1994; Weller, 1988). Behaviours are also traded-off against each other, for instance, resting and vigilance will show an inverse relationship with feeding (Aissaoui et al., 2011; Berl and Black, 2013) and therefore the productivity of a foraging patch will influence the time-activity budgets of the birds within it. Environmental conditions such as food availability, seasonality, location, tides, temperature, and wind also affect behavioural energy budgets (Weller, 1988). Previous studies investigating the diurnal time budgets of free-living wildfowl have revealed several behavioural trends useful to the evaluation of captive bird activity. In an analysis of non-breeding waterfowl, Weller (1988) noted that across a wide range of species (and with data recorded across a diurnal and 24 hr period) wildfowl can spend 20–70% of their time foraging, 10–50% resting, < 20% of their time on maintenance, vigilance and locomotion, and only 2% or less on social activities. The wide range of foraging and resting times most likely equate to species-specific differences, with herbivores species spending longer foraging and less time resting and fish-eating species, more time resting and less time foraging. These two activities are also the most frequent diurnal behaviours reported. Similarly, social, alert, maintenance, and locomotive behaviour were again found to account for only a small proportion of activity budgets in research conducted by Döpfner et al. (2009).

1.1. Aims

Captive wildfowl are an underused resource for research into behaviour and ecology of waterbirds (Portugal et al., 2010), therefore our study aimed to i) evaluate the normal behaviour budget values for wild ducks and ii) compare these data to observed values on the time-activity patterns of captive ducks of different species.

2. Methods

Data collection took place from 2015 to 2018 at three WWT Wetland Centres. WWT Slimbridge, Gloucestershire UK; WWT Arundel, West Sussex, UK and WWT London, Greater London, UK. The dates of data collection at each centre and the species (including total sample population) observed are provided in Table 1. For each season (i.e., spring/summer), for each year and for each centre, a different observer collected behavioural data. Each observer was trained by the first author to record and identify duck behaviour patterns specific to that species either in person (Slimbridge and London Wetland Centres) or via video footage of bird behaviour (Arundel Wetland Centre). Observers provided data for review by the lead author after one month of observations to check on data quality and validity. For each species and at each wetland centre, state behaviours, i.e. those of a long duration that can be measured as a moment of time (Martin and Bateson, 2007), were recorded using a standardised ethogram (Table 2). These state behaviours were foraging, resting, maintenance, social, alert, locomotion and abnormal. Abnormal behaviours were considered as poor welfare indicators if they occurred frequently (i.e., every four minutes of a

Table 1
Information on the study species and locations (plus observer ID for that date and location) used for data collection.

Year	Location	Dates / Observer initials	Enclosure	Species / Sample size
2015	Slimbridge	6th April-9th July AR	South American Pen	Chiloe wigeon *(Mareca sibilatrix)* / 40
			Tundra Pen	European goldeneye *(Bucephala clangula)* / 54
			Back from the Brink	European goldeneye *(Bucephala clangula)* / 6
2016		5th April-15th July SB	Australian Pen	Australian white-eye *(Aythya australis)* / 28
			North American Pen	Hooded merganser *(Lophodytes cucullatus)* / 22
			Asian Pen	White-headed duck *(Oxyura leucocephala)* / 12
			South American Pen	Black-bellied whistling duck *(Dendrocygna autumnalis)* / 32
				West Indian whistling duck *(D. arborea)* / 15
	Arundel	26th April-27th July SH	Mývatn Pen	Common scoter *(Melanitta nigra)* / 16
				Harlequin duck *(Histrionicus histrionicus)* / 2
				Long-tailed duck *(Clangula hyemalis)* / 24
	Slimbridge	11th November-10th January MT	Tundra Pen	European goldeneye/ 54
			Australian Pen	Australasian shoveler *(Spatula rhynchotis)* / 21
2017	Slimbridge	3rd April-13th July CG	Back from the Brink	Northern shoveler *(S. clypeata)* / 18
				Northern pintail *(Anas acuata)* / 19
				Eurasian wigeon *(Mareca penelope)* / 28
2018	London	28th May-1st August JT	African Wetlands	White-faced whistling duck *(D. viduata)* / 13
			Pantanal Wetlands	Fulvous whistling duck *(D. bicolor)* / 3
			Coastal Wetlands	Common eider *(Somateria mollissima)* / 6
				Northern pintail/ 12
			Wild birds	Mallard *(Anas platyrhynchos)* / abundant (c100)
				Tufted duck *(Aythya fuligula)* / abundant (c50)

five-minute period to differentiate from normal changes between short-term behaviours and erratic actions that may indicate excitement or short-term alarm. Discussion with PV and SH with their extensive practical knowledge of wildfowl activity enabled this benchmark to be decided upon). Abnormal behaviours were only recorded and analysed for captive birds. Extensive training of each observer, by the lead author, took place before data collection commenced each centre (and data checks continued during data collection) to ensure consistency in the identification of behaviour during each data collection period. Full details of how behavioural data collection was kept consistent is provided in Supplementary Information (Table S1).

2.1. Behavioural data collection (WWT Slimbridge)

Behavioural data for the creation of time-activity budgets was systematically recorded by hand on paper datasheets at three times of the day: session 1 (morning: 1000–1200 h BST), session 2 (early afternoon: 1300–1500 h BST), and session 3 (late afternoon: 1600–1800 h BST). Each session was split into 15 min observation periods. Within a 15 min observation period, an individual bird was focal followed and its behaviour recorded as an instantaneous scan (Martin and Bateson, 2007) every 1 min. A total of 8 birds (8 x 15 min) could be recorded within each session if all data collection went as planned and all birds remained in view.

The focal bird was chosen if it had not been knowingly previously sampled. Data from observations that did not complete a full 15-min sample (e.g., if the bird ceased to be visible as it swam out of view) were still included in analyses when proportions of behaviours performed were compared between individuals. Males and females, identifiable by their plumage or ringed leg (right leg for males, left leg for females) were sampled alternatively to obtain an equal number of each sex. For enclosures that allowed public feeding, when a bird was approached or fed by a visitor the observation was paused, and resumed when the visitor had withdrawn, to eliminate as much as possible any visitor influence on general time-activity patterns.

For autumn and winter data collection on Australasian shovelers and European goldeneye, the same focal follower for 15-min observations was conducted. Due to time constraints, one species was observed from 09:00 to 13:30 and the other from 14:00 to 16:30 on the same day of observation, with species alternating AM or PM for each subsequent observation day. The same observer collected all autumn and winter data.

Table 2
Ethogram of duck state behaviours used for the project by all observers across species.

Behaviour	Types
Foraging	The bird searches for and ingests food in a species-typical manner (including dabbling with the bill in shallow water, diving using the legs for propulsion underwater or and grazing on land using the bill to crop grass whilst walking, standing or sitting). Birds may forage on natural food (e.g. pond plants) or on grain provided by the WWT centre.
Resting	The bird is loafing (a period of reduced activity that occurs around midday), standing (not alert or vigilant but conscious and upright) or sleeping (the bird is standing or sitting but with "head tucked under wing" pose. One eye or both eyes may be closed).
Maintenance	Preening (including stretching and scratching) and bathing. The bird cleans and oils its feathers, using its bill and/or feet to manage the integrity of its plumage. Bathing occurs when the bird enters the water, and partially submerges, scooping water over its feathers using its head, neck and wings.
Social	Including: Courtship (species-specific reproductive behaviour from the male to female and vice versa), antagonistic and agonistic (aggression interactions such as biting, chasing, pecking or threat display), affiliative (interactions with a positive connotation such as pair-following, mate-guarding, allopreening or other species-specific social behaviours indicative of a non-aggressive social relationship).
Alert	The bird is vigilant to its immediate surroundings, scanning the environment with one or both eyes, usually with the head raised to assess the cause of any alarm (e.g. an anti-predatory behaviour).
Locomotion	The bird moves around the enclosure by swimming (paddling on the surface of the water using its feet), walking (movement on land by placing one foot in front of the other), scooting (fast movement across the water's surface using the feet and wings) and running (fast paced version of walking actions).
Abnormal	Repetitive, invariant behaviours that serve no obvious purposes or function: i) Boundary pacing (the bird walks up and down a fence line several times over, for example 4 min out of a 5 min period). ii) Attempt flight the bird repeatedly attempts to fly by launching itself into the air.

2.2. Behavioural data collection (WWT Arundel)

Behavioural data collection was conducted using the same approach as for WWT Slimbridge except for slight time changes for sessions 2 and

3: session 2 (13:00–15:15) and session 3 (16:00–17:30). To prevent any bias in observation behaviours, the noon observation period had a break in data recording from 14:00 until 14:15 since a talk for public (where ducks were fed) took place during this period. The afternoon recording session was half an hour shorter than the other two recording sessions owing to the centre closing at 17:30 and the researcher needing to leave the site at closing time. Each species was observed for one day per week, with long-tailed ducks being observed on one day and then both scotors and harlequin ducks being observed on the same day (fewer individuals of these two species compared to the long-tailed ducks). Weather and climate data were collected for each observation day using the online meteorological database (WorldWeatherOnline.com) for the corresponding area of Arundel, West Sussex.

2.3. Behavioural data collection (WWT London)

Behavioural data collection was conducted using the same approach as for WWT Slimbridge except for time changes for sessions 2 and 3: session 2 (12:45–14:45) and session 3 (15:30–17:30). Temperature and cloud cover were measured at the beginning of each time period using WorldWeatherOnline.com for the area of Barnes, Richmond-Upon-Thames. Daily visitor number was provided by WWT London for the total number of visitors on site. Each sampling day took place between Monday and Friday. At least one day every week was dedicated to a captive species, while the rest were spent observing the free-living species.

2.4. Behavioural data collection (WWT London wild birds)

Wild birds were observed in the nature reserve areas that surround the captive collection at WWT London, with the observer seated on benches or in hides at the wetland areas used by these wild birds. The same scan sampling technique for 15 min (using 1 min sample points) was employed for each individual wild bird before a brief rest period and a new bird (treated as a new, unique focal follow) was chosen for observation. To determine time spent flying, an approximation was decided upon whereby if a focal bird flew away and out of sight during the sampling period, it was assumed any remaining time left of the observation would be in flight (locomotion). Normal behavioural recording resumed if the bird took flight, and the behaviour post-flying was then observable. The timeframe for data collection was 09:30–11:30; 12:30–14:30; 15:30–17:00.

To determine the commonest behaviours (i.e., those that take up the largest proportion of the time-activity budget) performed by the wild birds observed, data were compared to the captive literature to see if wild birds can provide relevant evaluation of captive bird behaviour patterns. Comparison of directly collected data from wild birds was also compared to data from the literature to identify any potential location-specific (e.g. possible impacts on behaviour from the habitat these birds were in) or population-specific influences (e.g. possible behavioural influences due to sex ratio or population size) on the time-activity budgets of these wild birds.

The LWC was chosen as the site of wild bird data collection due to convenience and the recruitment of a research student local to the centre that could complete behavioural observations. Wild birds at the LWC could travel between wild areas (nature reserve) and areas of the living collection, across a range of wetland habitats.

2.5. Meta-analysis of the published literature

Using Google Scholar and the online repository Web of Science (https://wok.mimas.ac.uk/) observers AR, SB, CG and SH added to a cumulative list of published papers by using the search terms *wildfowl, duck, time-activity budget, time budget, activity pattern, behaviour, behaviour, waterfowl* during their specific year of observations. At the end of the data collection period, MOB completed the list of published students to 31st December 2018. Duplicates were checked for and any removed and only research articles that had observed wild duck behaviour and that provided information on the time spent on state behaviours were included in the final analysis. Peer-reviewed papers were the primary literature type selected but conference proceeding, where written up and formally published, were also included in the sample of literature. Following Prisma guidelines (Page et al., 2021), full text articles were read to ensure they provided relevant data. Articles were excluded if the full text could not be accessed. The final list of articles (N = 89) analysed are included in Supplementary Information Table S2.

2.6. Data analysis

A total of 777 h (equating to 32.3 days) of observation of captive ducks was undertaken plus 74 h of wild duck direct observation, across all species. For data taken from published wild studies N = 89 papers were selected. All data were analysed in R Studio v. 1.4.1106 (RStudio Team, 2021) via the statistical package R v. 4.0.2. (R Core Team, 2020).

2.6.1. Ecological differences

To analyse the average time activity budget of the wild behavioural data presented in Table S2, species of duck were grouped into categories of dabbling ducks (e.g., *Anas spp.*), seaducks (highly maritime species), diving ducks including stifftails (highly aquatic species such as pochards, *Aythya spp.* and *Oxyura spp.*) and then "other" (species that did not fit any of the preceding categories, including *Dendrocygna spp., Aix spp.* and *Tadorna spp.*). Standard error was calculated for each category of duck for each state behaviour. Behaviours were not normally distributed. Therefore, the commonest three state behaviours (foraging, resting and locomotion) across all categories of duck were evaluated for any significant difference in time of spent on that behaviour and category of duck using Kruskal-Wallis tests in RStudio. Post-hoc testing was conducted using the "dunn.test" function from the FSA package (Ogle et al., 2021).

2.6.2. Wild species differences

A general linear model was run for each of the state behaviours identified from the literature, using the species as the predictor variable. Any subspecies entries were reclassified as their full species. Species with limited ecological difference (e.g., the scoters, *Melanitta spp.*, were all group together). Species with fewer than three records were not included in the analysis. Rationalising these data in this manner provided a dataset of 76 records for 16 species, and all were results from studies on wild birds. The "plot(model name)" function was run to check the model fit based on the plot of residuals against fitted values and the normal Q-Q plot of standardised residuals against theoretical quantiles, and the r^2 value was assessed to determine variation captured by each model. Models were run using the grouping of species into rationalised categories (as the predictor variable) and the percentage time reported on each specific behaviour as the outcome variable. Where needed, post-hoc testing was conducted using the "lsmeans" and "pbkrtest" packages in RStudio (Halekoh and Højsgaard, 2014; Lenth, 2016).

2.6.3. Captive behaviour

For all captive species, a repeated measures model, using the LmerTest package (Kuznetsova et al., 2016) was run in RStudio, and significance determined using Staterthwaite's method (Koster and McElreath, 2017) by using the "anova(model name)" function. The enclosure that the birds were housed in ("Pen") was included as a random factor and the date of observation was a random factor too. Temperature (^{o}C), humidity (%), visitor number (daily count), time of day, season (spring or summer), sex of the bird (male, female or unknown) and species were included as fixed factors, and key state behaviours (foraging, resting/inactive, social, alert and movement) were the outcome variables. Rates of abnormal behaviour were incredibly low (1.6% of all responses) and were not included in any modelling.

Collinearity was checked using the "car" package (Fox and Weisberg, 2019) in RStudio and predictors with a variance inflation factor > 2 were excluded from the model (The Pennsylvania State University, 2018). The conditional r^2 value for this model was calculated using the MuMin (Bartoń, 2013) package in RStudio. Plots of the model residuals were assessed to gauge model fit. Post-hoc testing to identify species differences, season and time of day differences was completed using the same method as described for wild species differences.

For populations of the same species housed in different enclosures within the same centre or across two different locations, a further activity budget was drawn and Kruskal-Wallis testing employed to determine any significant difference between populations of these species.

2.6.4. Observation of wild behaviour

After reviewing plots of the standardised residuals for the behavioural data of the wild tufted ducks and mallard ducks from the London Wetland Centre a Generalised Additive Model (gam) was applied using the package "mgcv" (Wood, 2017) and gam function in RStudio. The behaviour of the birds was included as the output variable with species, time of day, season, sex, visitor presence, temperature and humidity included as potential predictors. Visitor number, temperature and humidity were included in the model as smoothed terms.

2.6.5. Autumn and winter behaviour

Data were collected during autumn and winter 2016–2017 on two species of captive wildfowl at WWT Slimbridge (European goldeneye and Australian shoveler). The same repeated measures testing was used to analyse sex, species and seasonal differences (fixed factors) on activity (outcome variable) with date and time being included as random factors.

2.6.6. All records of duck behaviour

The mean time (pooled across all species) spent on specific state behaviours taken from the published data set (meta-analysis), plus those directly collected wild data and directly collected captive data were compared using one-factor Chi-squared tests and illustrated in a final activity budget.

3. Results

3.1. Published wild studies: ecological differences

Supplementary Table S2 provides information on the individual amount of time spent on state behaviours for species included in published studies. Fig. 1 shows that foraging, resting and locomotion take up the largest proportion of the time-activity budgets of wild ducks in these published studies. Kruskal-Wallis tests for the category of duck against individual records of time on each behaviour showed there to be a significant difference between categories for average time spent resting (H= 17.57, df= 3, $P < 0.001$), on locomotion (H= 10.24, df= 3, P = 0.02) and foraging (H= 8.44, df= 3, P = 0.04) for the four categories of duck.

Post-hoc testing identified dabbling species as spending less time resting compared to diving ducks (Z value= −3.681, P = 0.001). Diving ducks spent more time resting compared to seaducks (Z value= 3.618, P = 0.002). Dabbling ducks spent more time on locomotion compared to seaducks (Z value= 3.065, P = 0.014). Finally, dabbling ducks spent more time foraging compared to diving ducks (Z value= 2.622, P = 0.05).

3.2. Published studies: species differences in the wild

Significant differences in foraging time were highlighted at the species level ($F_{15, 60} = 2.69$, $r^2 = 0.25$, P = 0.003) with scoters spending significantly more time foraging compared to all others (estimate= 23.85, SE= 11.54, t value= 2.07, P = 0.04). White-headed ducks showed a trend for less time foraging compared to other species (estimate= −21.04, SE= 10.95, t value= −1.92, P = 0.056).

Time spent resting was also significantly different between species ($F_{15, 60} = 4.57$, $r^2 = 0.42$, $P < 0.001$). White-headed ducks spent significantly more time resting than all other species (estimate= 32.44, SE= 8.96, t value= 3.15, P = 0.002). Ferruginous ducks and marbled duck may also be more inactive than other species as the results for these ducks tended towards significance (ferruginous estimate= 17.32, SE= 8.96, t value= 1.93, P = 0.058 / marbled estimate= −1.15, SE= 8.39, t value= −0.14, P = 0.059). Finally, the result for blue-winged teal show

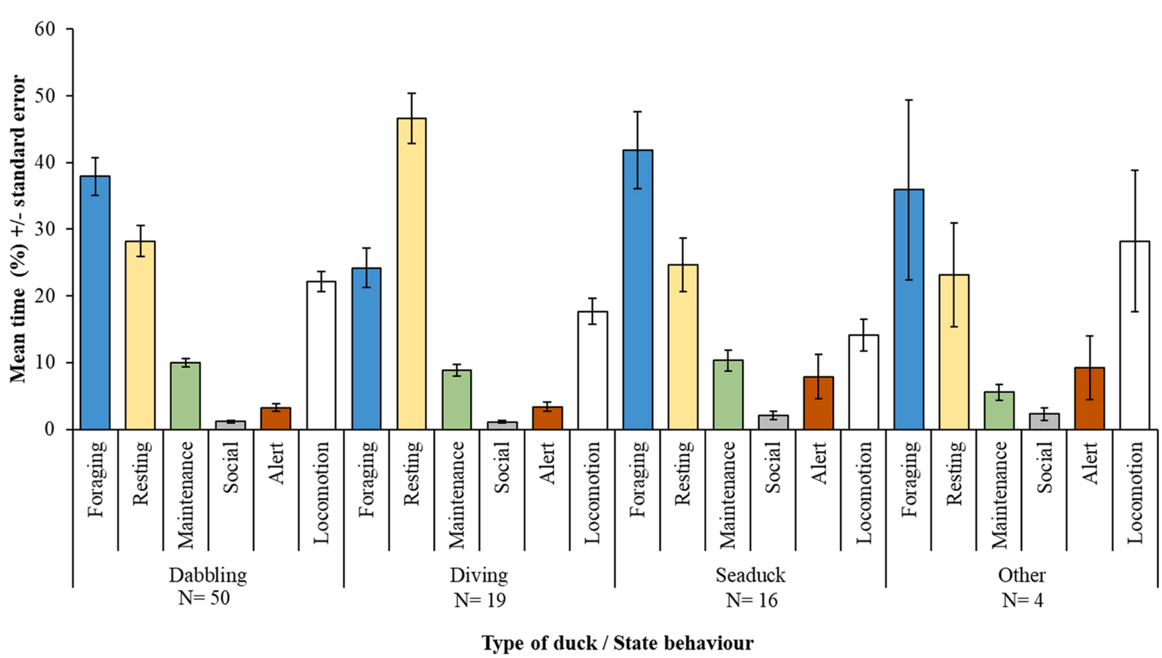

Fig. 1. Average time-activity budget from published data (see Table S2) for dabbling, diving, sea and "other" duck species (shelducks, Tadorna spp., whistling ducks, Dendrocynga spp., and perching ducks, Aix spp.). Foraging, resting and locomotion take up most of the time during the bird's day. Based on a sample of 89 records across 28 species.

a trend for less time resting than the other species in this sample (estimate= −17.44, SE= 8.98, t value= −1.94, P = 0.057). Overall, there were differences time spent on locomotion between species too ($F_{15,\ 60}$ = 1.96, r^2 = 0.16, P = 0.035) but no species-specific estimates were significantly different from this model. Differences in time spent on alert behaviours was noted from the analysis ($F_{15,\ 60}$ = 5.88, r^2 = 0.50, P < 0.001), with long-tailed ducks and northern pintail spending more time alert compared to other species (long-tailed duck estimate= 28.08, SE= 3.86, t value= 7.27, P < 0.001 / pintail estimate= 7.50, SE= 3.39, t value= 2.21, P = 0.031). There were no significant differences in time spent on social ($F_{15,60}$ = 1.44, r^2 = 0.08, P = 0.161) or maintenance ($F_{15,\ 60}$ = 0.70, r^2 = −0.06, P = 0.775) behaviour between species.

3.3. Captive behaviour

Overall, captive ducks spent 42% (± 0.007) of the time resting, 19% (± 0.005) of the time on maintenance behaviours (e.g., preening), 17% (± 0.004) of the time on movement (swimming, walking), 16% (± 0.005) of the time foraging, social behaviours at 3% (± 0.003) and alert behaviour at 3% (± 0.002) and stereotypic activities at < 0.1% (± 0.0002) of daily time budgets (Fig. 4). Supplementary Table S3 outlines the mean time spent on behaviour for each of the captive species observed for this research. Species differences are noted in the partitioning of time to each state behaviour but overall similar trends in the performance of commonest behaviours (resting, maintenance, locomotion) are clear. Differences are also apparent between the commonest state behaviours performed by wild ducks compared to captive birds, and between the observational data on wild ducks and that collected from the literature. Based on the sample of literature on wild duck time-activity patterns collated, data on ring-necked duck *(Aythya collaris)* was used as the comparison to the tufted duck due to the evolutionary similarity of these two species (Hollister, 1919) and the quality of behavioural data in our sample of literature.

Table 3 shows that environmental and zoo-specific variables impact duck behaviour (e.g., visitor number) as well as characteristics of the birds themselves (e.g., sex of the individual). Model estimates for continuous predictors showed that: Maintenance behaviours increased with increasing temperature (estimate= 0.07, SE= 0.02, df= 135.04, t ratio= 3.58, P < 0.001) and with increasing humidity (estimate= 0.01, SE= 0.007, df= 192.87, t ratio= 2.04, P = 0.04). Alert behaviour decreased with increasing temperature (estimate= −0.05, SE= 0.02, df= 308.93, t ratio= −2.75, P = 0.006). Movement increased with increasing visitor number (estimate= 0.0004, SE= 0.0002, df= 125.74, t ratio= 2.05, P = 0.043). Resting decreased with increasing humidity (estimate= −0.03, SE= 0.01, df= 299.98, t ratio= −2.25, P = 0.03). Post-hoc testing to identify where differences occur for significant categorical predictors are found in the supplementary information Table S4.

3.3.1. Location-specific differences in behaviour

For two captive species, northern pintail and common goldeneye, observations were conducted on birds in two different locations (pintail at WWT Slimbridge and WWT London) and in two different enclosures. Common goldeneye in the Tundra Pen and in the Back from the Brink enclosure at WWT Slimbridge. Supplementary Table S3 provides complete details on behaviour for these (and all other) flocks.

Enclosure and location factors were likely to influence the behaviour of the birds being observed. Fig. 2 shows that pintails in population 1 spent more time resting (H= 18.73, df= 1, P < 0.001) and more time foraging (H= 8.81, df= 1, P = 0.003) than birds in population 2. Pintails in population 2 were also significantly alert for longer than birds in population 1 (H= 82.54, df= 1, P < 0.001). For the goldeneyes, birds in population 1 spent significantly more time foraging (H= 27.04, df= 1, P < 0001) and significantly less time on locomotion (H= 6.45, df= 1, P = 0.011) than birds in population 2. These goldeneyes were not recorded as displaying alert behaviour.

Table 3
Modelling potential predictors of behavioural outputs in captive ducks. Significant values highlighted with *.

Behaviour	r^2 value	Predictor	F value	DF	P value
Foraging	36%	Species	7.95	15, 2	0.12
		Sex	0.70	2,	0.50
		Time of day	0.93	1560.57	0.40
		Season	0.32	2,	0.57
		Temperature	0.001	3088.09	0.98
		Humidity	1.03	1, 119.65	0.31
		Visitors	2.23	1, 170.55	0.14
				1, 368.98	
				1, 124.99	
Resting/ inactive	37%	Species	4.15	15, 2	0.21
		Sex	3.71	2, 1302.6	0.02*
		Time of day	2.37	2,	0.09
		Season	0.72	3086.54	0.40
		Temperature	0.15	1, 116.66	0.70
		Humidity	5.05	1, 155.01	0.03*
		Visitors	1.02	1, 300.0	0.31
				1, 130.13	
Maintenance	8%	Species	3,76	15, 2	0.23
		Sex	1.19	2,	0.31
		Time of day	1.19	1100.74	0.30
		Season	0.13	2,	0.72
		Temperature	12.80	3063.31	< 0.001*
		Humidity	4.17	1, 105.75	0.04*
		Visitors	0.002	1, 135.04	0.97
				1, 192.90	
				1, 157.58	
Social	74%	Species	1.27	15, 2	0.53
		Sex	11.98	2,	< 0.001*
		Time of day	3.35	1111.26	0.04*
		Season	6.51	2,	0.01*
		Temperature	0.21	3085.50	0.64
		Humidity	0.33	1, 89.89	0.57
		Visitors	1.50	1, 120.29	0.22
				1, 236.00	
				1, 100.07	
Alert	79%	Species	5.47	15, 2	0.17
		Sex	69.19	2,	< 0.001*
		Time of day	8.05	2668.18	< 0.001*
		Season	0.70	2,	0.41
		Temperature	7.54	3071.55	0.01*
		Humidity	0.005	1, 113.51	0.95
		Visitors	0.13	1, 308.93	0.72
				1, 831.65	
				1, 114.84	
Locomotion	39%	Species	10.09	15, 2	0.09
		Sex	3.80	2,	0.03*
		Time of day	8.14	1551.65	< 0.001*
		Season	1.81	2,	0.18
		Temperature	2.06	3087.99	0.15
		Humidity	0.0003	1, 120.08	0.99
		Visitors	4.18	1, 170.70	0.04*
				1, 366.47	
				1, 125.74	

3.4. Observations on wild birds

Table 4 shows that male ducks rested more than females and that tufted ducks rested more than mallards. Birds were less alert in summer compared to spring. Birds moved around more in summer compared to spring, with mallards moving more than tufted ducks and male birds moving less than females.

Comparing the significant smoothed terms in Table 4 against plots of the model output shows significant influences of environmental factors on wild duck behaviour. Maintenance behaviour increased with humidity, social behaviour declined with increasing visitor presence, alert behaviour declined with larger numbers of visitors present but movement significantly increased, and movement declined with increasing humidity.

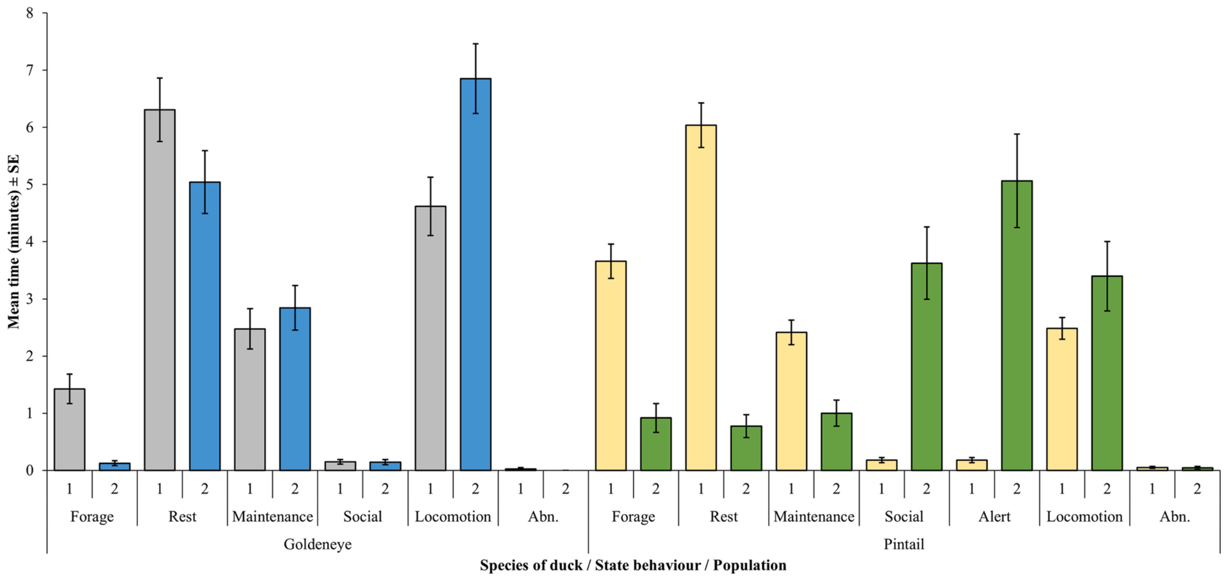

Fig. 2. Comparison of two captive populations of common goldeneye at WWT Slimbridge (1 = Tundra Pen; 2 = Back from the Brink) and comparison of captive northern pintails at two locations (1 = WWT Slimbridge; 2 = WWT London). Abn. = abnormal behaviour.

Table 4
Significant outputs for coefficients and smoothed terms from a generalised additive model for potential predictors of behavioural performance in wild ducks at the London Wetland Centre.

Behaviour	Model r^2 value	Predictor	Estimate	Standard error	T value	P value
Resting	11%	Species (tufted duck)	0.74	0.27	2.75	0.006
		Sex (male)	0.88	0.21	4.25	< 0.001
Alert	13%	Season (summer)	-2.81	1.29	-2.19	0.03
		Species (tufted duck)	3.96	0.84	4.71	< 0.001
Movement	16%	Season (summer)	2.74	0.99	2.76	0.006
		Species (tufted duck)	-2.24	0.60	-3.74	< 0.001
		Sex (male)	-1.47	0.37	-3.98	< 0.001
Smoothed terms						
Behaviour	**Model r^2 value**	**Predictor**	**F value**	**Effective df**	**P value**	
Maintenance	12%	Humidity	2.78	2.66	0.04	
Social	14%	Visitor number	3.23	6.41	0.003	
Alert	13%	Visitor number	14.87	1.67	< 0.001	
Movement	16%	Visitor number	9.53	1.98	< 0.001	
		Humidity	2.97	7.94	0.004	

3.5. Autumn and winter activity

No occurrences of abnormal repetitive behaviours were recorded during wintertime data collection. Very low occurrences of abnormal repetitive behaviour were observed for goldeneye and shoveler during spring and summer (see Table 4). Significant differences in species and behaviour to support the time-activity budget presented in Fig. 3 are provided in Table 5.

3.6. Comparing all data

Data taken from the sample of published literature shows that free-living ducks spent most time foraging, resting and moving (Fig. 4), whereas captive birds were most likely resting or performing maintenance behaviours. The wild birds directly observed were mostly seen alert or socialising. Overall rates of abnormal behaviour in captive birds were negligible.

There was no significant difference between mean time allocated to maintenance between the published sources, wild data and captive data ($\chi^2 = 3.23$, N = 45.6, df= 2, P = 0.20) or for locomotion ($\chi^2 = 2.64$, N = 48.04, df= 3, P = 0.28). Captive birds spent significantly more time resting and inactive compared to wild ducks ($\chi^2 = 24.03$, N = 80.26, df= 2, P < 0.001). Finally, captive ducks were significantly less likely to be alert than wild counterparts ($\chi^2 = 44.47$, N = 41.38, df= 2, P < 0.001).

An overall summary of key results from this entire research project is provided in Fig. 5.

4. Discussion

This research has identified that environmental, temporal and sex variables significantly influenced the performance of specific behavioural states in captive ducks. The meta-analysis of published data on wild ducks showed that ecology and species significantly affected daily behavioural budgets alongside of seasonal and sex differences. Behaviour of captive birds over spring and summer differed from that observed over autumn and winter, with resting and maintenance behaviours occurring more in spring/summer than autumn/winter (for example). Whilst species was not a significant predictor of behaviour in these captive birds, descriptively, times spent on some behavioural states varies by species (Supplementary Table S3). Movement is the behaviour with the closest trend to being significant (Table 3). Resting, locomotion and maintenance were the commonest behaviours performed by captive ducks but differences by ecological niche (i.e., dabbling ducks, diving ducks, sea ducks) were apparent- diving ducks were the most inactive of all species observed. No reports of abnormal repetitive behaviours were noted from published works and none were identified from direct

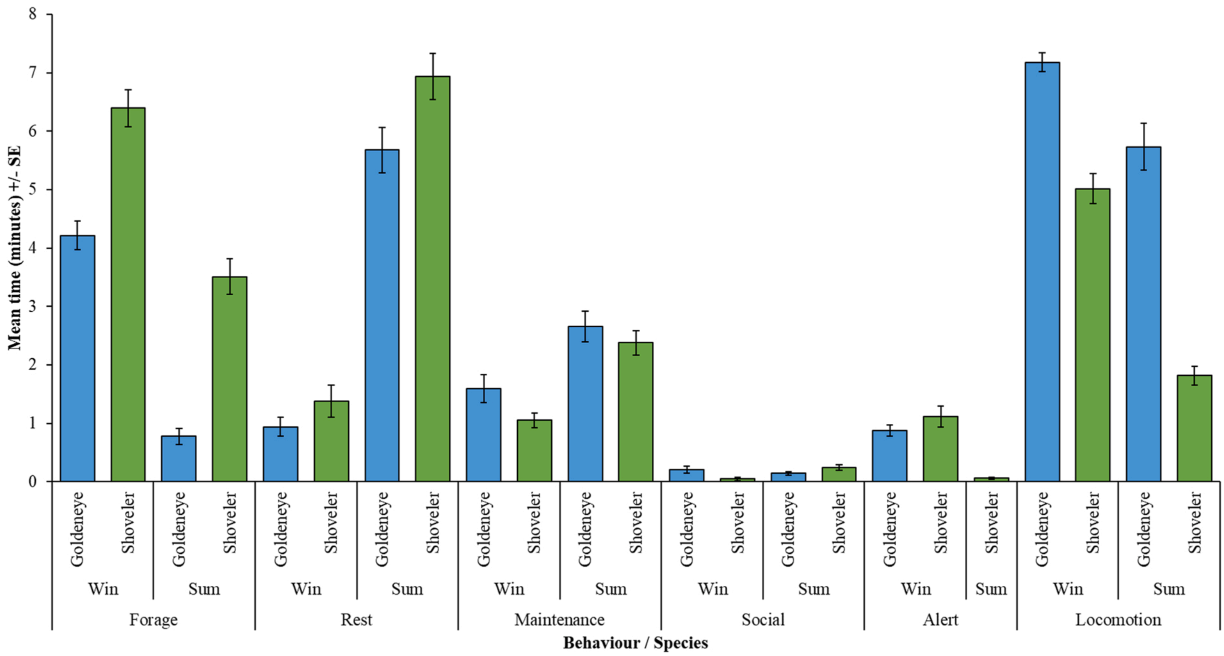

Fig. 3. Time activity pattern for a representative species of diving duck (common goldeneye) and dabbling duck (Australasian shoveler) for the autumn and winter period of 2016–2017 ("win") compared to spring and summer ("sum") behavioural data for common goldeneye (from 2015) and northern shoveler (2017).

Table 5
Significant model outputs and post-hoc comparison for autumn-winter data compared to spring-summer data for shoveler and common goldeneye housed at WWT Slimbridge.

Behaviour	Significant predictor	Model r^2 value	F value	DF	P value
Foraging	Season	30%	38.48	1, 35.26	< 0.001
	Species		45.76	1, 174.60	< 0.001
Resting/ inactive	Season	25%	55.03	1, 33.33	< 0.001
Maintenance	Season	7%	14.45	1, 30.48	< 0.001
Social	Sex	18%	12.80	1, 709.4	< 0.001
Alert	Season	25%	58.51	1, 36.79	< 0.001
Movement	Season	26%	14.07	1, 31.28	< 0.001
	Species		38.81	1, 195.8	< 0.001
Post-hoc testing					
Behaviour	**Comparison**	**Estimate**	**SE**	**t ratio**	**P value**
Foraging	Summer – winter	-3.12	0.50	-6.20	< 0.001
	Goldeneye – Shoveler	-2.59	0.39	-6.67	< 0.001
Resting/ inactive	Summer – winter	5.18	0.70	7.42	< 0.001
Maintenance	Summer – winter	1.17	0.31	3.80	< 0.001
Social	Female – male	-0.14	0.04	-3.76	< 0.001
Alert	Summer – winter	-0.96	0.13	-7.65	< 0.001
Movement	Summer – winter	-2.37	0.63	-3.75	< 0.001
	Goldeneye – Shoveler	2.81	0.46	6.14	< 0.001

behavioural observation of wild birds. Performance of abnormal repetitive behaviour was incredibly low in captive ducks (and indeed absent in some species) with the highest recorded occurrence of 0.4% of a population's overall time activity budget.

4.1. Comparing behaviour of wild and captive ducks

Whilst behaviour only provides one way of understanding welfare, the negligible amount of time spent on abnormal repetitive behaviour suggests that these captive ducks are not filling their diurnal time budgets with stereotypy due to restrictions on movement (Fig. 4). High resting rates in captive populations, however, are worthy of further investigation. Although resting rates are high in captivity, wild ducks can spend a large proportion of their time budget resting too (Fig. 1). Exploration of higher rates of maintenance behaviours and inactivity would lead to better understanding of any impact on bird health and wellbeing caused by captive management, as presently we are unable to determine whether this lack of activity is a potential negative welfare indicator.

Although abnormal behaviour is not readily apparent, resting and lethargy may be an indication of a poor quality, generic environment that does not allow for maximal behavioural diversity in daily activity pattern. The specific type of inactivity may inform on internal affective states that can illustrate negative or positive welfare (Fureix and Meagher, 2015)- further assessment of individual bird inactivity across species will provide the context for this inactivity (lethargy or contentment, for example) to increase the contextualisation of these time-activity budgets. Research in laboratory mice has shown that animals being awake but inactive do not have to be performing stereotypic behaviour to potentially be demonstrating a behavioural indicator of poor welfare (Fureix et al., 2016), especially if the animals are housed in a barren or non-enriched environment. Such ideas may be supported by the lack of significance of species as a predictor of behavioural differences between duck species. The age, sex, population characteristics, size and shape of the enclosure and husbandry routine of the WWT centre housing the birds may account for this. Similarly, a snapshot of activity during the normal visitor opening period for each wetland centre will not provide information on a complete behaviour pattern or time budget (and therefore welfare states) across the full 24 h period, and these data should be collected in a future project.

Social group and enclosure size may play a role in mitigating any

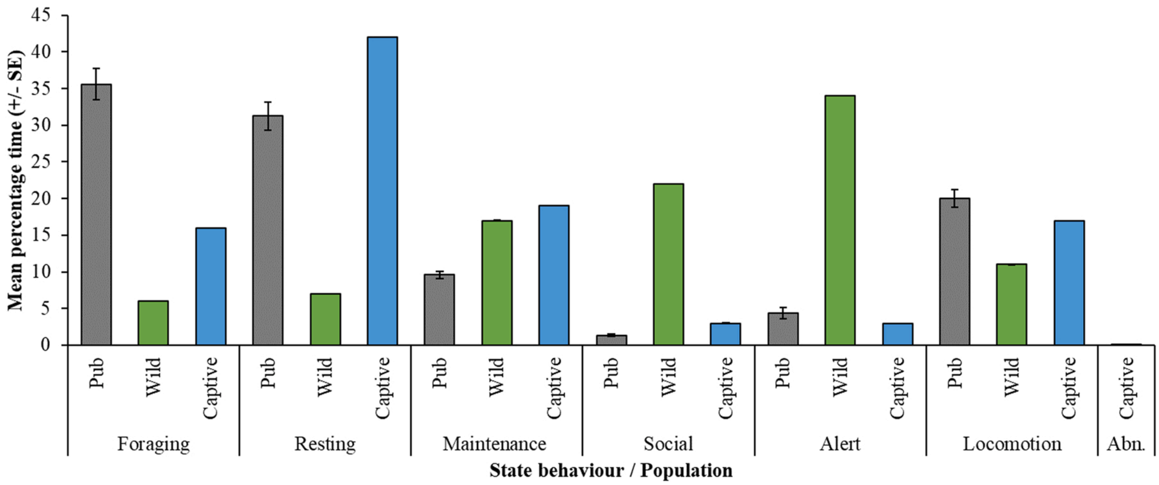

Fig. 4. Comparison of average time per day spent on behavioural performance for all species of wildfowl. Pub= published literature (grey bars), Wild= wild birds directly observed at the London Wetland Centre (green bars), Captive= birds held in the animal collections across WWT centres (blue bars). Abn= abnormal behaviour. Standard error included on all bars, but very little variation is noted for captive and wild observed birds.

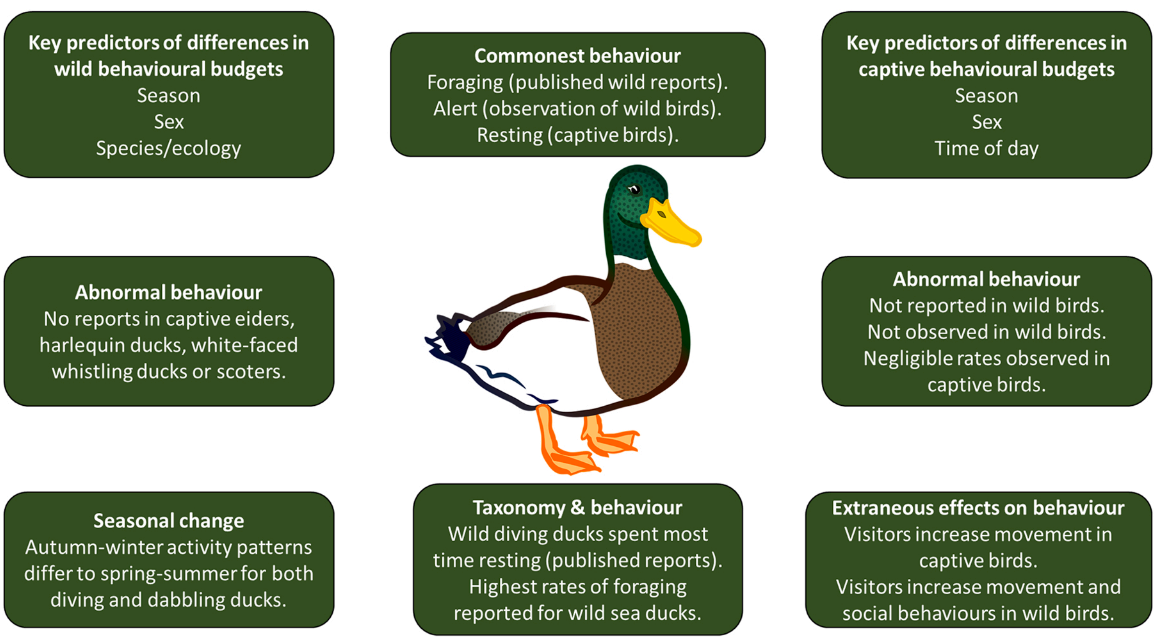

Fig. 5. Summary of key findings from the data analysis across all sources of behavioural data (published studies and direct observation).

performance of abnormal behaviour in captive ducks. For example, common goldeneye kept in the larger of the two flock sizes displayed no abnormal behaviour. No abnormal behaviour was performed by common eiders housed in a social group that provided numerous opportunities for male-female display, or in the flock of white-faced whistling that included both adult males and females to facilitate social interactions. Embedding ecological knowledge into the management captive ducks, by developing and designing the birds' enclosures on their natural behaviour patterns may further promote positive welfare states.

4.2. Future work, limitations, and extensions

Further consider of the species included in the study and how they were sampled could provide more data to turn general trends into significant differences. Identification or marking of individual birds to ensure focal follows are consistent and to reduce unwanted repeats of the same individuals caused by a lack of individual identification may provide more robust flock-wide time budgets that would statistically support any variation in species' behaviour illustrated in Table S3.

Extension of this work should include the collection of behavioural data on fully winged ducks in aviaries to quantify time spent off the ground (in flight and perching). Comparison of the same species, housed in an aviary and in an open enclosure, would provide information on use of height and choice of flying as a means of locomotion. Such data could then be evaluated against that collected on flight-restrained bird to further assess what portions of daily time budgets are restricted by flight restraint. This research extension would be especially valuable to advancing our understanding of the welfare of migratory species or those species that spend time arboreally, e.g. whistling ducks and "perching ducks" (e.g., mandarin, *Aix galericulata*). Previous research on pinioned mandarins identified a limited daily time-activity budget, comprising of short periods of feeding in between longer periods of preening and resting (Bruggers and Jackson, 1977). This lack of behavioural diversity could be attributed flight restraint limiting behavioural choice.

The logistical constraints of implementing this research project meant that a spring-summer data collection period had to be used for most of the observations on captive birds (and all data collection on wild birds). Consequently, influences of physiological changes on behaviour (e.g., moult) as is noted in previous work on captive ducks (Portugal et al., 2010) is likely to have impacted upon data collection towards the end of the summer period. The dates chosen for direct observation data collection each year attempted to maximise spring and early summer observations to eliminate as much as possible any potential effect of the moult on bird activity. Seasonal variation in behaviours is identified in Table 5, suggesting that this is an important variable to consider whenever one is inferring duck welfare from behavioural measures.

A potential visitor effect may be apparent on these ducks as increased movement of captive ducks (at higher visitor numbers) may be attributed to extra feeding by visitors. Likewise, increased movement of wild ducks may be a response to higher visitor numbers and associated decreases in vigilance caused by birds moving away from larger numbers of people. Quantifying behavioural changes associated with human presence on captive and wild ducks would provide helpful information on potential stressors and welfare impacts.

4.2.1. Methodological developments

Any further study should consider the validity of behavioural observation techniques and formalised measurement of interobserver reliability (IOR). Whilst extensive training of all observers was conducted prior to data collection, and data quality managed throughout observations, inclusion of IOR would add further validation of the methods employed and these resulting data (Bateson and Martin, 2021). Given that species of duck has consistently been identified as an non-significant predictor of behaviour, it is likely that IOR is relatively high (each observer observed a different species, therefore if IOR was low one might expect 'species' to be a significant predictor due to variation in observer identification of behaviour at each sample point). Training of observers is crucial; Wark et al. (2021) emphasise the need for reliability testing alongside of live and video-based training opportunities to ensure observers can follow a standardised ethogram accurately. As the observers completed live and video-based training using a standard ethogram, confidence in data is likely to be high.

Further extension to this work needs to further quantify time spent in flight, as wild ducks may not have always remained airborne based on our estimation of behavioural performance in the field. Some species of duck resort to flight as an escape response more readily than others; e.g., teal species spring into the air in defence (Guillemain and Elmburg, 2014) whereas pochard species are likely to dive underwater (Austin et al., 2017) and therefore differences in reliance on flight as a response to a stressor needs more investigation. Similarly, human presence and influences on time-activity patterns should be scrutinised, with data collection including foraging time when birds are fed by visitors compared to days when visitors are not present or at different levels (e.g., high or low overall numbers). Visitor feeding was not measured in this study to standardise behavioural data collection across all exhibits- some that allowed public feeding and some that did not. In-depth research on specific enclosures that contain the same species but differ in allowing public feeding or not would provide valuable information on how much of an impact public feeding has on captive duck activity patterns.

The social grouping of birds (i.e., being in a flock) has not counted as a social state as this is was a passive and not an active performance of behaviour. Consequently, adapting the methods to record the behaviour of each bird as, for example, social (foraging) or social (resting) or solitary (foraging) could provide more information on the overall time spent in a social group and therefore on social activities. Direct observation of wild ducks showed higher rates of social behaviour compared to captive and published wild data (Fig. 4). Focussing on common, native species within one wetland location, where habitat is plentiful and of good quality (and foraging is easier) may have increased the number of ducks in a given area, therefore increasing opportunities for social interaction. Further investigation of the type of social activity being performed in the context of the environment (quality of habitat and number of birds present) would further aid the interpretation of social behaviour between sample populations.

Finally, developing how abnormal repetitive behaviours were recorded to include short duration event behaviours (Bateson and Martin, 2021) could potentially capture more instances of stereotypy if it was being performed. As chronic stressors can decrease activity as well as cause prolonged performance of invariant, repetitive behaviours (Gormally and Romero, 2020) measuring bouts of event behaviour in sequences (Tyler, 1979) could enable short duration actions to be accurately displayed in a time-activity budget, providing further information on behavioural responses to stressors.

5. Conclusions

This research has identified negligible to zero performance of behavioural indicators of poor welfare in captive ducks across different species housed at different facilities. Whilst some aspects of time-activity patterns are dissimilar between wild and captive ducks (notably reduced foraging in captive birds), the large amount of time spent resting by captive ducks is mirrored, in part, in data from published literature. Resting in captive ducks may be a response to a more controlled environment where food is readily available and hence the need for extensive foraging is reduced. Wider impacts of inactivity on bird welfare, considering measurement of space and resource usage within an enclosure, would be a logical research extension. Several species, including whistling ducks and eiders, displayed no abnormal behaviour, and these species may be more suitable candidates for captive living when maintained in diverse and ecologically relevant social groups that provide choice and control over their behaviour patterns (remembering that behaviour is only one measure of welfare state). Changes to husbandry and management (e.g. variable feeding schedules or enhancing opportunities for social choice within a flock) could positively influence behavioural diversity- increasing activity levels and providing a more engaging environment for the birds and the visitors that come to see them. Cross-institutional research to compare behaviour in enclosures that house ducks fully winged would enable comparison with our data on these flight restrained species. Such research could evidence i) the importance of flight to captive ducks and ii) good practice in enclosure design that can facilitate performance of all behaviours with resulting welfare improvements.

Ethics

All data were observational and followed the best practice as set out by the Study of Animal Behaviour (ASAB)'s guidance on animals in research. Each separate project was reviewed by the relevant University ethics committee and all methods were reviewed by WWT's Animal Welfare and Ethics Committee (AWEC) at time of development.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Thank you to Dr Baz Hughes and Dr Ruth Cromie for supporting the original inception of this research. Thanks to Mr Marc Boardman, Mr Mark Simpson and Ms Sally Airey for review of the final project output. We are grateful to three anonymous reviewers for their considered, kind and helpful comments that have been so important to development of this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2022.105626.

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