Variability in the breeding season of Black Swans *Cygnus atratus* in southeast Queensland, Australia

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Abstract

Variability in the duration of the breeding season and the mean number of annual breeding attempts recorded for Black Swans *Cygnus atratus* in southeast Queensland, Australia, were evaluated in relation to environmental variables. There was a significant correlation between the extent of the breeding season (measured as the number of months in which eggs were hatched) with both the number of breeding attempts made by paired birds in that year and also the number of territorial pairs recorded. This may reflect changes in the timing of breeding by individual pairs to reduce competition for favoured breeding and foraging locations. The number of breeding attempts per territorial pair in any one year was influenced primarily by summer rainfall and the Southern Oscillation Index (SOI), with higher values for both of these environmental variables being associated with more breeding attempts and increasing numbers of breeding pairs. We therefore suggest that the increasing numbers of breeding pairs, and also the increasing numbers of breeding attempts associated with more favourable weather conditions, may have led to the longer breeding seasons recorded for Black Swans in southeast Queensland in recent years.

Key words: Black Swan, breeding attempts, breeding season, Queensland.

In the northern hemisphere, four of the five swan species are strongly migratory with the timing of their migration and breeding influenced by daylength as well as environmental conditions (Rees *et al.* 2019), and the onset of egg-laying is thought to be entrained to photoperiod for many northern hemisphere waterfowl (Murton & Kear 1978). In contrast, southern hemisphere swan species including the Black Swan *Cygnus atratus* are more nomadic and move opportunistically to ephemeral wetlands to breed when these become available (Kingsford *et al.* 1999; Rees *et al.* 2019). This opportunistic response to environmental conditions leads to highly nomadic behaviour in Australian waterfowl (Roshier 2006), with a number of studies attributing variability in the start of the breeding season to rainfall and flooding, which result in the appearance of wetland breeding habitats and stimulates breeding behaviour (Briggs 1992; Halse & Jaensch 1989). Water levels are known to influence the timing of breeding by waterbirds (Braithwaite & Frith 1969), with rainfall, flooding and tidal patterns creating breeding habitat and encouraging plant growth. Braithwaite and Frith (1969) found that the most important consequence of water level changes was modification of the food supply, which in turn affected the breeding season for several species. Other studies have also shown that food supply (Dalby *et al.* 2014) and temperature (Serventy & Marshall 1957) are important for the timing of breeding by waterfowl, with a limited food supply known to reduce breeding activity (Kingsford & Norman 2002). The Southern Oscillation Index (SOI) – a measure of fluctuations in air pressure between the western and eastern tropical Pacific – has additionally been linked to variation in breeding patterns, with more breeding events occurring in years with a high index value for Australian land birds (Gibbs *et al.* 2011) and for waterfowl (Duursma *et al.* 2018; Norman & Nicholls 1991). SOI is used to give an indication of the development and intensity of El Niño and La Niña events with low SOI index years indicating drier El Niño type conditions in Australia. High SOI index years have milder, wetter conditions which lead to increased vegetation for feeding (Norman & Nicholls 1991) and more ephemeral sites for breeding (Kingsford *et al.* 1999), which in turn result in more intense breeding events (Vilina *et al.* 2002).

The Black Swan is a large waterfowl species native to Australia (Marchant & Higgins 1990) with a large, introduced population in New Zealand (Williams 1981). The species is known to respond to rainfall as a trigger for breeding (Halse & Jaensch 1989), with water levels and resultant food availability additionally important for determining the timing of breeding (Braithwaite & Frith 1969). The extent to which these factors influence the overall duration of the breeding season however remains less well understood.

Brisbane, in southeast Queensland has a humid sub-tropical climate with hot humid summers, which occur at the same time as northern hemisphere winters, and warm winters which correspond with the northern hemisphere summer. Mean maximum summer temperatures range from 28.0–29.1°C with mean winter temperatures ranging from 21.0–22.1°C with less rainfall over the winter period (Bureau of Meteorology 2024). Previous studies have shown that the swans can nest throughout the year both in New South Wales (Marchant & Higgins 1990) and in southern Queensland (Coleman 2014) when conditions are suitable, whilst breeding occurs from March (following the tropical wet season) in northern Queensland, and from May–October in coastal New South Wales (Marchant & Higgins 1990). The Black Swan has a more clearly defined breeding season (from July–October) in New Zealand, although this can be more variable in colonial nesting birds. In Northland, New Zealand, the birds nest in two waves, with the first wave commencing in September and the second in March, significantly extending the breeding season (Marchant & Higgins 1990).

Here we describe breeding by Black Swans monitored on the Gold Coast, Queensland, Australia over a 15-year period and analyse factors influencing the duration of their breeding seasons, with a view to explaining variation in the swans' breeding phenology. Whether the duration of the breeding season is associated with the number of breeding attempts by territorial pairs and the swans' productivity is also considered.

Methods

Black Swans have been studied in coastal southeast Queensland since 2007, in an area of approximately 3,200 km^2 extending from Brisbane south through the Gold Coast Region to the New South Wales border (Coleman 2010, 2014; Coleman *et al.* 2021). The study area and methods, which have been described previously (Coleman 2014), involve year-round, monthly monitoring of both breeding and non-breeding birds in the region. Each month a fixed route was travelled through the study area visiting suitable swan habitat. The birds on those sites were counted with territorial pairs recorded. For paired birds, breeding histories were built through observations made of swans on their territories, with the month of breeding noted and the number of cygnets hatched and reared recorded for each breeding bird. Almost all nests located were on man-made water bodies, associated with housing or golf courses, with smaller numbers located on tidal channels. In addition to natural food, most of the birds responded to human handouts and supplementary feeding by humans (with *e.g.* bread, lettuce and corn provided) was common.

During the monthly surveys, attempts were also made to catch and ring as many unmarked birds as possible. The swans were caught by hand, using bread or grain to attract them close enough to capture, and were fitted with two leg rings: a standard Australian Bird and Bat Banding Society metal ring on one leg and a red plastic ring (each engraved with a unique code in white characters) on the other. The latter facilitated multiple re-sightings of individuals over time without the need to recapture them. Swans were caught for banding in every month of the year and a total of 1,239 were birds banded between January 2007 and December 2022, with catch numbers ranging from 38–157 birds *per annum*. Each swan caught was aged (based on its plumage characteristics), sexed by cloacal examination and weighed to the nearest 0.1 kg. As many ring codes as possible were read during the surveys so that the life histories of the colour-marked birds (including their age on first breeding, number of breeding attempts and breeding success) could be built up over time.

Response variables

For breeding birds, the month in which cygnets were hatched was used as a means of recording the length of the breeding season (*Breeding Season Extent*) in each calendar year, expressed as the number of months in which cygnets were recorded hatching. More precise estimates of hatching date were not possible because field visits were made only once a month. The number of breeding attempts for each territorial pair in the study area (*Breeding Attempts per Pair*) was also calculated for each year, by dividing the number of breeding attempts by the number of territorial pairs recorded in that year. A breeding attempt was recorded when a territorial pair was seen to be incubating eggs. In some years, pairs were recorded having two or more breeding attempts (Coleman 2014). This provided two annual measures of the breeding season: *Breeding Season Extent* – a measure of breeding phenology, and *Breeding Attempts per Pair* – a measure of breeding propensity.

Predictor variables

Variables described in earlier studies as influencing breeding by waterbirds in Australia, examined as potentially influencing breeding by Black Swans in the current study, were: *Solar Exposure* (MJ/m^2), *Rainfall* (mm), *Maximum Temperature* (°C) and *SOI*. Each of these variables were summarised by year and season, with the austral summer (December–March) and non-summer months (April–November) seasonal data used in the analysis: summer data to evaluate environmental conditions prior to the peak in breeding, and non-summer data to evaluate the influence of environmental conditions during the peak breeding period and beyond (Fig. 1). While both annual and seasonal environmental variables were included in the single variate analyses, annual environmental variables were removed from the GLM analysis to ensure that the influence of seasonal environmental variables were evaluated appropriately. Mean values were used except for rainfall, with the total rainfall recorded for each period being used.

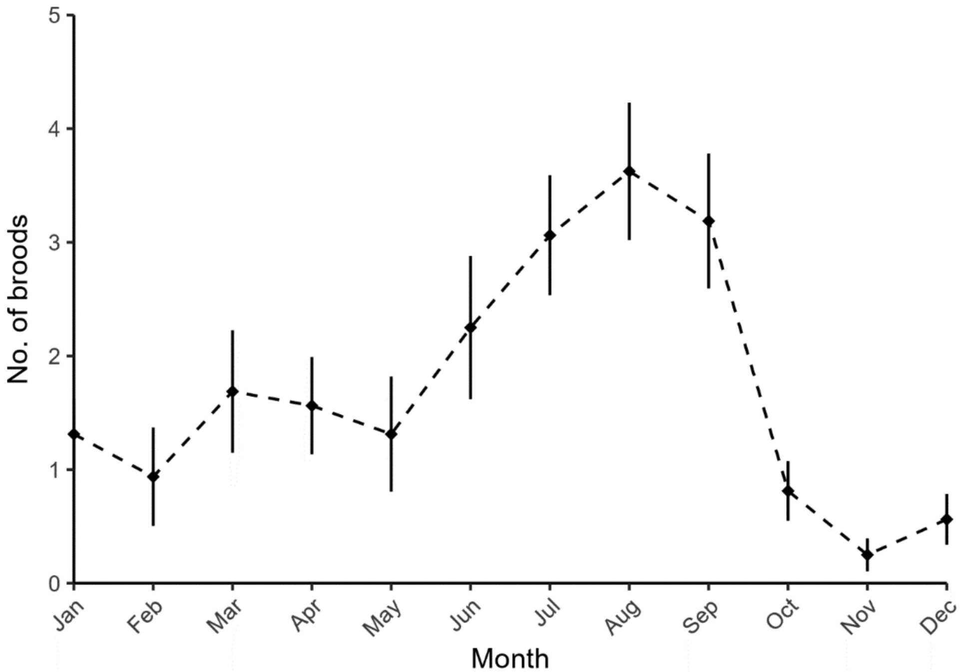

Figure 1. Months in which pairs were recorded hatching cygnets in southeast Queensland from 2008–2022, expressed as the mean number of broods (± s.e. bars) hatched per month over the study period.

SOI has a broadscale association with climate in Australia, with eastern parts of Australia (which include this study area) being drier and warmer in years with a low SOI value and with cooler, wetter conditions in years with higher SOI values. The other predictor variables differ more regionally in Australia. For instance, solar exposure is typically higher in inland regions in comparison with our study area, being lower in tropical and temperate zones because of increased cloud cover in the wet season (tropics) and at more southerly latitudes. Southeast Queensland receives more annual rainfall than inland areas at the same latitude and more southerly locations in Australia, but less than locations in tropical Queensland. Temperatures in southeast Queensland are typically warmer than more southerly locations but cooler than tropical Queensland and the interior, with the latter also experiencing more temperature extremes.

These weather data were obtained from the Gold Coast Seaway station (Station ID No. 040764 on the Australian Bureau of Meteorology website), located in the centre of the study area. In addition, the number of territorial pairs present in the study area were counted each year. Number of territorial pairs was included as a predictor variable to establish whether an increasing number of pairs might also be influencing breeding season phenology.

Data analysis

Linear regression analysis using R 4.2.3 (R Core Team 2023) was used to establish any significant relationships between each of the response and predictor variables (Supporting Materials Table S1). Time variables were organised using the "lubridate" package (Grolemund & Wickham 2011) and results of the regressions were displayed using the package "ggplot2" (Wickham 2016). The total variance explained by seasonality was also calculated by creating a time series of the number of broods recorded per month, throughout the study period. This was then seasonally decomposed using the stl ( ) function in base R to show the seasonal component, *i.e.* the variation within the dataset between each seasonal cycle (Cleveland *et al.* 1990).

Generalized linear models (GLMs) were run using the software package StatsDirect (version 3.6.6) with the identity link function to determine the predictor variables that best explained variation in the number of breeding months (*Breeding Season Extent*), with a separate model used to explain the variation in the mean number of breeding attempts recorded per pair each year. Predictor variables were first checked for collinearity through a correlation matrix, but no collinearity was found, so all were included in the initial model except for the annual environmental variables which were removed to ensure the influence of seasonal environmental variables were not impacted by the annual figures. Non-significant variables were then sequentially removed from the model until the most parsimonious model was achieved.

Results

The Black Swans were found to hatch cygnets in all months of the year during the study (2008–2022), but with a marked peak in hatchings recorded from June–September (Fig. 1). However, the number of broods per month was highly variable between both years and months, with seasonality explaining only 24% of the variation. The number of months in which cygnets hatched during a calendar year (*Breeding Season Extent*) ranged from as little as three months in some years to 11 months in other years, whilst the number of breeding attempts per territorial pair ranged from 0.30–1.33 (range = 0–5) over the 15 years of the study.

The number of months in which birds were recorded breeding within any given year correlated significantly with the number of pairs present in the study area (linear regression: $F_{1,13}$ = 6.37, P = 0.03; Fig. 2), with the slope indicating that for every additional pair in the population, the number of breeding months increased by 0.09 (2.73 days) or by one month for every additional 11.56 pairs recorded. With the exception of total number of breeding attempts ($F_{1,13}$ = 17.86, P = < 0.01), none of the other variables tested individually showed a significant correlation with the duration of the breeding season.

The annual number of breeding attempts per territorial pair (*Breeding Attempts per Pair*) was negatively correlated with the mean annual solar exposure (*Solar Exposure – Annual*: $F_{1,10}$ = 7.34, P = 0.02; Fig. 3a), and the mean solar exposure from December to March (*Solar Exposure – Summer Months*:

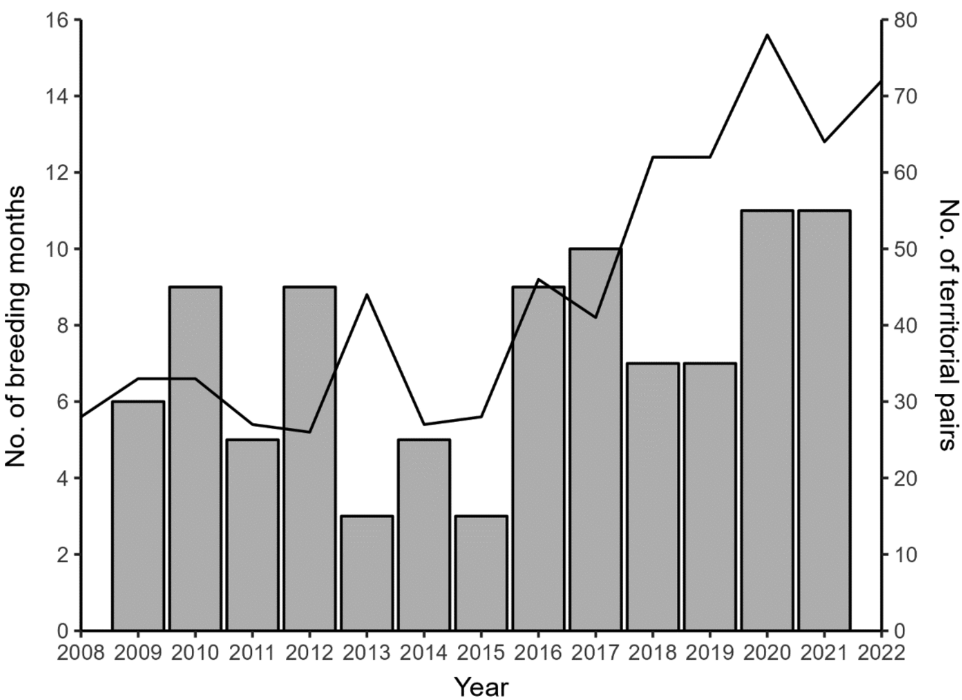

Figure 2. Number of breeding months (histogram) and number of territorial pairs (solid line) recorded for Black Swans in southeast Queensland each year from 2008–2022.

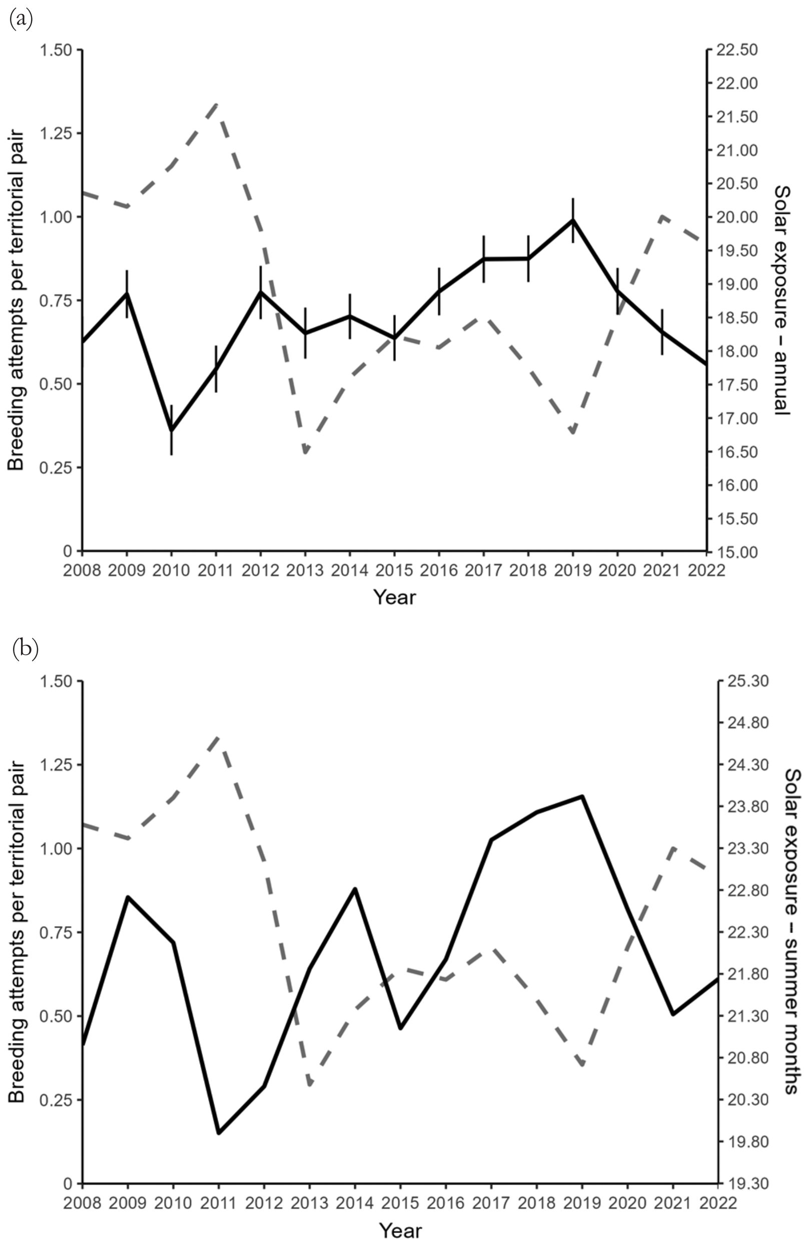

Figure 3. Number of breeding attempts per territorial pair of Black Swans (dotted line) overlayed with the mean solar exposure recorded over: (a) the year (solid line), and (b) the austral summer (December–March; solid line), from 2008–2022. Note: s.e. values for summer solar exposure are very small, so not showing.

$F_{1,13}$ = 8.05, P = 0.01; Fig. 3b). There was also a strong significant positive correlation for the number of breeding attempts with the total rainfall recorded in the austral summer (*Rainfall – Summer Months*: $F_{1,13}$ = 10.22, P = 0.01; Fig. 4a), and a significant correlation with rainfall over the rest of the year (*Rainfall – Non-Summer Months*: $F_{1,13}$ = 6.07, P = 0.03; Fig. 4b). The number of breeding attempts each year was additionally associated with mean SOI values, both for the year in question (*SOI – Annual*: $F_{1,13}$ = 9.65, P = 0.01) and on considering the peak breeding and non-breeding seasons separately (*SOI – Summer months*: $F_{1,13}$ = 6.72, P = 0.02; *SOI – Non-Summer Months*; $F_{1,13}$ = 5.28, P = 0.03; Figs. 5a,b). None of the other tests showed either a significant positive or negative correlation with the annual number of breeding attempts per territorial pair (Supporting Materials Table S1)

A GLM analysis provided further insights into the variables that best predicted the extent of breeding season (full initial model in Supporting Materials Table S2) and the number of breeding attempts (Supporting Materials Table S3). For the duration of the breeding season only the number of breeding attempts by all territorial pairs in the study area provided significant correlation (Table 1). For the number of breeding attempts per territorial pair, the most significant predictor variable was the total number of territorial pairs recorded each year, with the total number of breeding attempts also being significant (Table 2).

Discussion

The long-term data on Black Swans breeding in southeast Queensland indicated that the number of territorial pairs has increased since 2008, and that this corresponded with an increased duration of the breeding season, expressed as the number of months in which cygnets were recorded hatching. Coleman (2014) has previously reported that the number of paired birds rose during the early years of the study from 2007 to 2010 but then declined to the lowest number in 2012. From 2012 the number of paired birds has increased through to 2022, and the breeding season extent has been consistently longer in the latter years of the study (Fig. 2).

The Black Swan is known to nest territorially (Marchant & Higgins 1990), and birds in this study area nested on an extended network of saltwater and brackish water channels and interconnected lakes. Pairs held breeding territories while nesting but after hatching often then ranged widely throughout the network of canals and waterbodies until their cygnets fledged. While no assessment of the availability and uptake of suitable nesting habitat was conducted, it may be possible that human and tidal impacts on the shorelines of these waterbodies meant that birds were limited by suitable nesting sites, constraining the number of pairs breeding at any one time and extending the breeding season. Certainly, there are usually several territorial pairs on popular breeding lakes and territorial fights are common (J. Coleman, pers. obs.). Anecdotal evidence from private landowners on those lakes with nesting swans, and the authors' observations of family groups, indicate that these pairs do nest at different times of the year and often very close to other nest locations once they have been

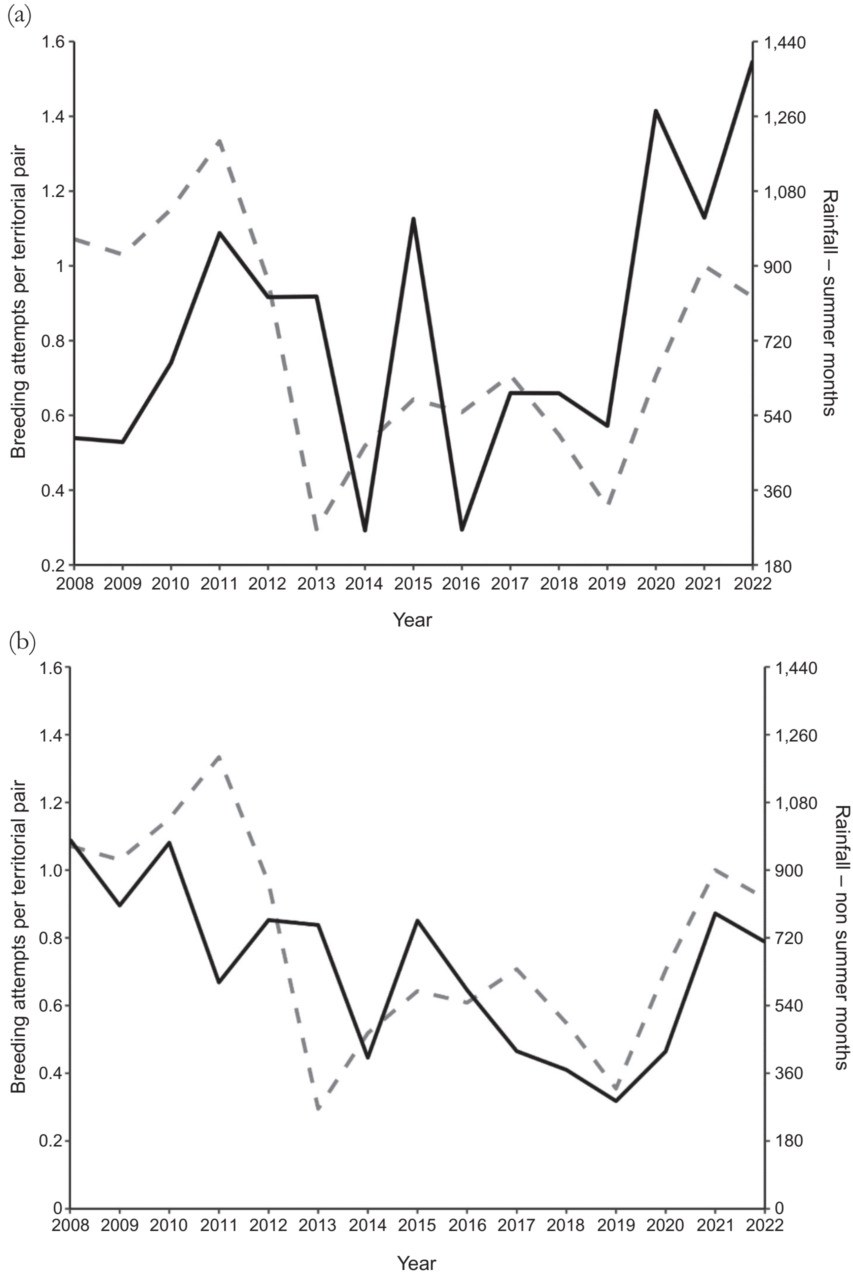

Figure 4. Number of breeding attempts per territorial pair (dotted line) overlayed with: (a) total rainfall (mm) in the austral summer (December–March; solid line), and (b) total rainfall in the remaining months of the year (April to November) from 2008–2022.

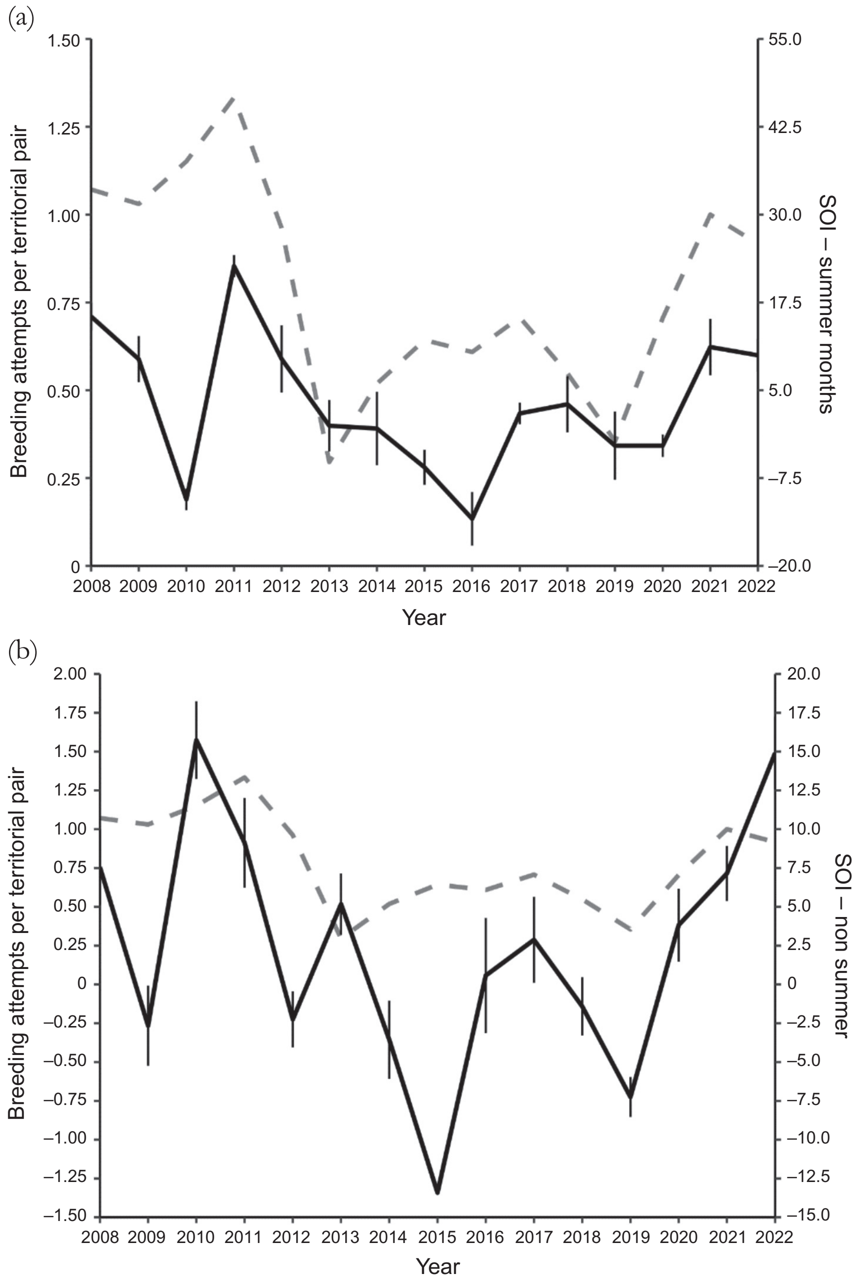

Figure 5. Number of breeding attempts per territorial pair (dotted line), overlayed with the mean annual Southern Oscillation Index for: (a) the austral summer (December–March; solid line), and (b) the non-summer months (April–November; solid line), from 2008–2022.

Table 1. Final most parsimonious Generalized Linear model (GLM) of the relationship between significant predictor variables and the extent of the Black Swan breeding season in southeast Queensland, Australia, from 2008 to 2022 inclusive. The full initial model is presented in the Supporting Materials (Table S2).

Predictor variable	**Coefficient**	***R***	$t_{1,13}$	***P***
Intercept	3.24		2.89	0.01
Total number of breeding attempts	0.13	0.76	4.23	0.01

Table 2. Final most parsimonious Generalized Linear Model (GLM) of the relationship between significant predictor variables and the number of breeding attempts per Black Swan pair per year in southeast Queensland, Australia, from 2008 to 2022. The full initial model is presented in the Supporting Materials (Table S3).

Predictor variable	**Coefficient**	***R***	$t_{1,13}$	***P***
Intercept	0.86		11.71	< 0.01
Number of territorial pairs	–0.02	–0.93	–9.18	< 0.01
Total number of breeding attempts	0.02	0.95	10.04	< 0.01

vacated by earlier breeders. However, the potential additional impact on the extent of the breeding season from increasing numbers of pairs utilising limited breeding sites requires more investigation as a causal factor, along with the potential effects of artificial feeding in these localised breeding hotspots.

The lack of an association with other environmental variables in the GLM was interesting and may reflect differences in the locations of the studies conducted. Previous studies in southwest Australia (Halse & Jaensch 1989) and New South Wales (Braithwaite & Frith 1969; Braithwaite 1982) were conducted on natural water bodies that experienced seasonal and longer-term periods of flooding and dry cycles, which had a significant effect on the swans' food supply which in turn impacted breeding ability. High SOI years and solar exposure are both typically associated with improved aquatic vegetation growth (Norman & Nicholls 1991). This would result in an extended breeding season, because of improved conditions for breeding birds allowing breeding for longer periods of the year. The locations studied in southeast Queensland were primarily artificial with permanently maintained water levels. Studies in New South Wales found that artificially maintained water bodies have less diversity and abundance in waterfowl species when compared to unregulated and ephemeral sites, with further investigation also showing reduced plant availability for herbivorous species in those regulated water bodies (Kingsford *et al.* 2004). In coastal southeast Queensland, while this may also have been the case for the permanent, regulated water bodies and channels, the birds' natural diet was supplemented with food from humans (J. Coleman, pers. obs.). This, along with the sub-tropical climate, may facilitate year-round breeding on such habitats, with only the number of breeding birds available and suitable nesting sites being limiting factors. This contrasts significantly with the breeding biology of inland birds which are reliant on ephemeral water bodies and far more influenced by environmental factors.

Further examination of the number of breeding attempts per territorial pair each year provided additional insights into the extent and frequency of breeding. While solar exposure had some negative influence on the number of breeding attempts per territorial pair, increased summer rainfall and SOI had more significant effects. Similar results have been found in other studies (*e.g.* Halse & Jaensch 1989), where summer rainfall was associated with increased food supply. Negative correlation with solar exposure is likely to reflect an inverse relationship with rainfall. Rainfall is a major trigger for breeding by most Australian waterfowl (Serventy & Marshall 1957; Braithwaite 1982; Halse & Jaensch 1989), and higher rainfall years would correspond with lower solar exposure due to cloud cover.

SOI was also significantly correlated with number of breeding attempts per year, with more breeding attempts in years with higher index values. Higher index values lead to wetter conditions in Eastern Australia, typically associated with El Niña activity, whilst negative values occur in times of drought (El Niño conditions). While clearly correlated to rainfall, only rainfall during the austral summer was significantly correlated with higher numbers of breeding attempts, while rainfall over the whole year was not. In the combined multivariate analysis, however, environmental factors became less relevant with the number of breeding attempts and number of breeding pairs being the primary influences on breeding season extent and breeding attempts per territorial pair. While this may suggest that more environmental factors may be at play, for example higher temperatures (which would also occur in the austral summer) are known to encourage the plant growth required for a successful Black Swan breeding season (Serventy & Marshall 1957), anthropomorphic factors such as artificial feeding may also mask the effects of environmental variables and need further investigation.

Conclusions

Black Swans in this study nested primarily on artificial waterbodies which are not subject to the changes in water levels and food availability that occur in more natural environments. Increasing numbers of breeding attempts, which were linked to increasing numbers of territorial pairs, appeared to be responsible for longer breeding seasons when conditions were suitable. Competition for nesting sites may have been a driver of the extension to the breeding season but this requires further investigation, as do effects on the swans of artificial feeding which is widespread in the study area. However, many other factors affect this species' breeding activity and productivity, with rainfall and SOI influencing the frequency with which birds nested in a single year. Increased breeding attempts during wetter years could also have had a compounding impact on the duration of the breeding season, with more breeding attempts leading to an extended breeding period as pairs rear cygnets and then renest. More offspring produced in years of multiple breeding attempts also increased the population further, impacting breeding season extent in future years as those offspring entered the paired population. If the number of paired birds continues to increase it will inevitably introduce density dependent effects in future years with competition for suitable breeding habitat increasing. This will almost certainly lead to birds dispersing further afield into areas with a lower density of territorial pairs.

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