## Divorce rates are stronger predictors of breeding success in little penguins compared to foraging behaviour and environmental factors

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## ABSTRACT

Factors affecting breeding success in seabirds result in indices that can be useful for predicting population reproductive output, without the need for invasive and intensive monitoring. Such factors include environmental conditions that affect prey availability and distribution, leading to variation in behaviours related to foraging effort, such as foraging trip duration. Further, social factors, such as divorce, may offer an opportunity for birds to seek a more suitable partner to enhance long-term reproductive success, but may negatively impact success in the short term. The relative importance of environmental, behavioural and social predictors on reproductive output is unclear, as these factors have seldom been examined in tandem. In this study, we investigated environmental factors at differing scales, alongside foraging trip duration and divorce rate, to examine the consequences on reproductive success over 13 breeding seasons in an inshore foraging seabird, the little penguin (*Eudyptula minor*). Population divorce rate proved to be the most useful predictor of reproductive success, with years of lower divorce associated with higher hatching and fledging success. Shorter foraging trip durations were associated with higher fledging success, but longer trips led to more successful hatching rates. After controlling for the effect of divorce, marine environmental conditions were not a strong predictor of breeding success in this study. Therefore, we propose that the divorce rate can be a powerful index and a valuable tool for predicting population level reproductive success for seabirds facing similar environmental and foraging pressures as little penguins.

**Key words:** Eudyptula minor, divorce, little penguins, foraging, reproductive success

## INTRODUCTION

Monitoring reproductive success in marine seabirds is important for understanding the viability of these populations. However, directly monitoring nests for fledgling output during a breeding season is labour-intensive and invasive, potentially putting vulnerable chicks at risk (Giese 1996). Hence, a more practical approach may involve monitoring other factors that are easier to measure and known to impact reproductive success. In seabirds, raising chicks relies on foraging effort and parental care in dynamic marine environmental conditions. This produces various environmental and behavioural indices that could be monitored to predict reproductive success. However, the relative usefulness of each index remains unclear because these factors have not been examined together.

Environmental factors on a global, regional and local scale determine ocean productivity, including food availability which is a vital resource for reproduction (Polis et al. 1997; Becker et al. 2007; Dave and Lozier 2010; Pelletier et al. 2012) and, therefore, monitoring environmental conditions may provide useful data to predict reproductive output of a population. Further, such information is generally readily available through online databases. At the global scale, the El Niño cycle can drive reduced prey abundance in ocean basins such as the Western area of the South Pacific Ocean (Ancona et al. 2012; Genovart et al. 2013), with the Southern Oscillation Index (SOI) predicting these events. Regionally, changes in Sea Surface Temperature (SST) can result from upwelling and reduce the input of nutrients supplying the growth of prey populations (Peck et al. 2004; Weeks et al. 2013). Higher SSTs can reduce prey availability for seabirds due to decreased productivity at lower trophic levels and increased movement of fish (Peck et al. 2004, Erwin & Congdon 2007, Afán et al. 2015). At the local scale, spatial distribution of prey can be altered through stratification of the water column and the presence of a thermocline can act as a thermal barrier to prey (Pelletier et al. 2012; Garthe et al. 2014; Meyer et al. 2020). Examples of ocean conditions at each scale showed altered foraging capacity in several species of seabird (wedge-tailed shearwater, *Ardenna pacifica*, Peck et al. 2004; Adélie penguin, *Pygoscelis adeliae*, Lescroel et al. 2009; little penguin, *Eudyptula minor*, Ropert-Coudert et al. 2009; blue-footed boody, *sule nebouxii*, Ancona et al. 2012; Cory's shearwater, *Calonectris diomedea*, Genovart et al. 2013) and can affect reproductive success (marbled murrelet, *Brachyramphus marmoratus*, Becker et al. 2007).

An essential behaviour for successful reproduction is foraging. Most seabirds are central place foragers that are obliged to return to land to care for their offspring, restricting their foraging range and duration (Schreiber and Burger 2001; Ichii et al. 2007). Unsuccessful foraging can be expensive for seabirds and can influence individual body condition, reproductive success and overall population dynamics (Boggs 1992; Chivers et al. 2012). The distance individuals must travel to access suitable foraging zones is particularly important, because birds that travel further to access a foraging zone must increase time away from their offspring (Terauds and Gales 2006; Boersma and Rebstock 2009; Saraux et al. 2011a; Jakubas et al. 2013) and their reproductive success can be lower when chicks are forced to wait for long periods between meals (Chiaradia and Nisbet 2006). Foraging trips durations may, therefore, reflect environmental conditions and represent a strong determinate of reproductive success. This is evident in the little penguin where long foraging trips led to slower growth rates of chicks and significantly reduced the number of fledged chicks per adult compared to years with shorter foraging trips (Chiaradia and Nisbet 2006, Joly et al. 2023).

Social behaviours, such as divorce rate within a population, may represent the cumulative outcome of environmental factors and foraging requirements on reproductive success. Continuing a pair bond over time is generally less costly than finding a new mate and reproductive success tends to increase with experience, at least in some species (Fowler 1995; van de Pol and Verhulst 2006; Sánchez-Macouzet et al. 2014). However, when pairs fail to produce fledglings (Setiawan et al. 2005), or where there are asynchronous arrival times of previous partners to the breeding site driven by environmental cues (Gunnarsson et al. 2004; Afán et al. 2015), they are more likely to divorce (Choudhury 1995; Setiawan et al. 2005). Divorce is potentially expensive and risky, at least in the short term, because during divorce, individuals must spend time finding and courting a new partner, possibly delaying egg production or not breeding at all (Gousy-Leblanc et al. 2023). This may consequently force parents to forage for their chicks during times of poorer food availability (Verboven and Verhulst 1996; Moody et al. 2005). While divorce is a tactic to improve reproductive success long-term, in years with higher divorce rates the population as a whole may experience a reduction in reproductive output (Gousy-Leblanc et al. 2023). Thus, divorce rates of populations may potentially be a good predictor of population reproductive output for the breeding season.

In this study we monitored the reproductive success of a colony of little penguins over 13 breeding seasons and investigated the relationships with environmental conditions, foraging trip lengths and divorce rates. Little penguins have one of the shortest foraging ranges (20km) of all penguins (Hoskins et al. 2008; Pelletier et al. 2014; Sánchez et al. 2018), and changes in foraging conditions are highly influential on their reproductive success (Chiaradia and Nisbet 2006; Saraux et al. 2011b; Amélineau et al. 2021; Saraux and Chiaradia 2022). Further, little penguins benefit from maintaining pair bonds, with pair longevity related to increased reproductive success (Nisbet and Dann 2009). We aimed to test the relative usefulness and importance of marine environmental factors, foraging behaviour and divorce rates on predicting reproductive success within a population. Using these data, we determined which measure is the best index for predicting reproductive success in a population, informing future research of the most reliable index for monitoring population reproduction for little penguins and possibly other seabirds.

## MATERIALS & METHODS

### Study site & monitoring protocols

We investigated little penguins at the Penguin Parade ® site of the megacolony located at the western end of Phillip Island, Victoria, Australia (38º 15’ S, 143º 30’E) with a population size of about 28,000 to 32,000 penguins (Sutherland and Dann 2012). Data from a study site of approximately 100 artificial nest boxes within the larger Summerland Peninsula were used over 13 breeding seasons (2000-2012), which provides a good proxy of the whole population (Sutherland and Dann 2014). Each year, ~70% of nest boxes were occupied (average number of pairs monitored 71.5, range 50 – 98). All penguins within the study colony were permanently identified with unique-numbered electronic transponders (Allflex Australia Pty Ltd, Capabala, Queensland) that were injected subcutaneously between the scapula (Chiaradia and Kerry 1999). Presence of adults within the study area was detected using a purpose-built handheld transponder reader and to minimize disturbance to the birds the reader was passed along the exterior surface of the walls of the nest boxes. Once birds began pairing and courtship was observed, this was considered the beginning of the breeding season and data collection began (Chiaradia and Kerry 1999). During the breeding season nest attendance was recorded three times a week and nests were checked for chicks and the different stages of breeding were recorded (Table S1 for definitions of breeding stages).

As measures for the population reproductive success (summarised in Table S1), we recorded the average number of eggs per breeding pair for the season, hatching success (proportion of eggs that hatched), fledging success (proportion of chicks that fledged) and the average number of fledglings per pair for the season. Chicks were considered to have successfully fledged upon reaching >45 days of age and being fully feathered since the last encounter (Chiaradia and Nisbet 2006). Monitoring within a season ended once all nest boxes were empty of pairs or chicks.

### Environmental variables

For global marine conditions, average values of monthly SOI from 2000-2012 from September to January (corresponding to the breeding season) were obtained from the Bureau of Meteorology, Australia (http://bom.gov.au). In the southern Australian climate, positive values indicate wetter conditions (moving towards La Niña), with cooler daytime temperatures, while negative values indicate drier and warmer conditions (moving towards El Niño).

Regional conditions were indicated by data for SST for the waters off Phillip Island, obtained from the US National Oceanic & Atmospheric Administration website (http://www.esrl.noaa.gov). *In situ* and satellite SSTs along with SSTs simulated by sea ice cover (Reynolds et al. 2002), were used to conduct optimum interpolation analysis (NOAA OI SST V2) to calculate the SSTs used in this study (giving regional conditions). Weekly SST data were averaged from September – January in the years 2000 to 2012, and averaged for a one-degree grid, 38 °S - 40°S x 143°E - 145°E (Cullen et al. 2009).

Data for local conditions were inferred from delta temperature (Δ T) using temperature profiles from Bluelink Ocean Data Assimilation (BODAS, Oke et al. 2007). To calculate Δ T, the surface temperature (0m) was taken from SST and temperature at 50m was subtracted as a measure of stratification in the water column (Oke et al. 2005; Oke et al. 2007). Data were weekly means in the 1 X 1 degree box defined by -38°S –39°S X 143.5°E – 145.5°E from September 2000 to December 2012.

### Foraging Trips

Foraging trip durations of individual penguins were determined using an Automated Penguin Monitoring System (APMS), developed by the Australian Antarctic Division (see Chiaradia & Kerry, 1999 for further details) and modified by Kean Electronics (https://www.kean.com.au/) that monitored colony attendance by birds. The APMS was located at the main colony entrance and when a bird crossed the weighbridge the reader recorded the transponder number, time and date (Kerry et al. 1993). To track the arrival and departure of individuals from the colony, the APMS recorded continuously over 13 breeding years from 2000 to 2012. Using the data from the weighbridge, we determined the duration of their trips in days. Only birds that had successfully fledged chicks were used when determining foraging trips, which vary over the post-guard stage and are critical for fledging success (Saraux et al. 2011b).

### Divorce rate

Divorce rate was calculated at a population level for each breeding season using the data from nest box monitoring by cross-referencing the presence of individual birds with their partners from previous seasons. We defined birds as being widowed or divorced depending upon whether the previous partner was seen again. Partners that did not reoccur within the dataset were considered to have disappeared, classifying the individual as widowed. Partners that returned during the monitoring period and paired with a different bird were considered to have divorced. As divorce rate could only be calculated by comparing pairings from previous years, the breeding season of 2000 (the starting year in this study) did not have a divorce rate assigned to it, meaning that this year could not be used in the models (resulting in a final sample size of 12 breeding seasons). Within-season divorce following a breeding attempt with a new partner in the same season is rare in little penguins, and was not observed in the Phillip Island colony during this study period.

### Statistical analysis

Four linear models were used to produce models that best explained the variance seen within the response variables (Quinn and Keough 2002). Response variables indicating reproductive success for each season were the average number of eggs laid per pair, hatching success (proportion of eggs hatched of eggs laid), fledging success (proportion of fledglings of chicks hatched) and the average number of fledged chicks per pair. Linear models were used on count data while generalized linear models were used to analyse proportional data with a binomial link function. Measured predictor variables considered were the environmental variables SST, SOI and ΔT, and the behavioural predictors mean foraging trip duration and divorce rate. Before building our models, we tested for collinearity between the predictors. Sea surface temperature was significantly higher with low ΔT (R = -0.91). As the R value exceeded the cut off 0.7 between these two variables, we excluded ΔT to avoid collinearity problems (Tabachnick and Fidell 2018). We removed ΔT instead of SST, as SST can have a robust effect on prey availability (Afán et al. 2015; Pelletier et al. 2014), while changes in Δ T can be overcome with behavioural tactics (Meyer et al. 2020). The final predictor variables included for each model were SST, SOI, mean foraging trip duration and divorce rate.

We used conservative Akaike Information Criterion values (AICc) for the model selection (Anderson and Burnham 2002). To further determine those factors that had the greatest importance within the models we used model averaging (Burnham and Anderson 2002; Symonds and Moussalli 2011). All models that had ΔAICc ≤ 6 were used in the model averaging with the MuMIn package in R (Burnham and Anderson 2002; Symonds and Moussalli 2011). If the top model was a subset of another retained model and did not provide a sufficient improvement in loglikelihood, we excluded the competing model to avoid over-weighting parameters during model averaging (Burnham and Anderson 2004; Arnold 2010; Grueber et al. 2011). All statistical analysis was conducted using R version 4.2.2 (R Core Team, 2022).

## RESULTS

Measures of reproductive success varied across the monitoring period (Figure S1) along with environmental marine conditions, foraging trip duration and divorce rate (Figure S2). Among these variables, divorce rate was significantly higher with decreasing SST (R = -0.69) (Table 1). No other variables used in the final models were significantly correlated.

*Number of eggs –* Over the monitoring period there was some variation in the number of average eggs produce by pairs each season (average = 1.93, range = 1.76 – 2.00, Figure S1a), with nine best-fit models (two were excluded due to uninformative parameters, Table S2). No environmental or behavioural measures significantly affected number of eggs laid by pairs (Table 2, Figure 1).

*Hatching success –* The proportion of hatched eggs across seasons was on average 0.79 (range 0.59 – 0.95) (Figure S1b). Five models were best-fit, with one removed for uninformative parameters (Table S3). In years of lower divorce rate and longer average foraging trip duration the hatching success was significantly higher (Table 3, Figure 2). The environmental variables did not affect hatching success. Divorce rate had the highest relative importance (R = 1.00), followed by foraging trip duration (R = 0.92).

*Fledging success –* Proportion of successfully fledged chicks across seasons varied widely across the monitoring period, with an average of 0.67 (range 0.30 – 0.87, Figure S1c). Lower divorce rates and shorter average foraging trip durations significantly increased success (Table 4, Figure 3), as found by two best-fit models (Table S4). Divorce rate, foraging trip duration and SOI all had equally high relative importance (R = 1.00, though SOI was not found to have a significant effect).

*Number of fledglings –* The average number of fledglings per pair each season varied across the monitoring period (average 1.03, range 0.52 – 1.58, Figure S1d). Nine best-fit models found that lower divorce rates tended to increase the number of fledglings (Table S5), but no predictor model significantly affected this (Table 5, Figure 4).

## DISCUSSION

Our study over 13 breeding seasons demonstrated that the population divorce rate was the most reliable predictor of reproductive success within a season in this little penguin population. When the divorce rate was low, hatching and fledging success was higher, highlighting the importance of stable pair bonds in improving reproductive outcomes. Shorter average foraging trip lengths also led to higher fledging success of chicks, while longer foraging trips increased the likelihood of eggs hatching. Marine environmental conditions did not significantly predict reproductive success once the effect of divorce was accounted for. These findings highlight the complexity of breeding success determinants at different stages and the critical roles of social stability and foraging behaviour in the reproductive ecology of little penguins.

### Reduced divorce rate increases reproductive success

Divorce rate was the strongest factor for predicting reproductive success in this population, with seasons of low population level divorce rates leading to an increased proportion of successful hatching and fledging. Little penguins and other seabirds that prolong their pair bond over multiple seasons are known to experience increased reproductive success over time (Black 1996; Kim et al. 2007; Nisbet and Dann 2009; Saraux and Chiaradia 2022). In contrast, divorce may also be an adaptive tactic to increase longer term reproductive success (Culina, Radersma and Sheldon 2015), especially where previous breeding success was low (Setiawan et al. 2005), a higher quality mate becomes available (Ens et al. 1993), or environmental events prevent or delay repairing (Gunnarsson et al. 2004; Afán et al. 2015). However, while divorce can improve reproductive output in the long term, it may have a negative effect on reproductive success in the short term (Gousy-Leblanc et al. 2023), as observed in this population. This is likely because the newly formed pairs have no breeding familiarity (Gousy-Leblanc et al. 2023)*.* Such patterns have also been observed in other species. Newly formed Australasian gannets (*Morus serrator*) pairs have a higher chance of reproductive failure compared to reunited pairs (Ismar et al. 2010). Blue-footed boobies (*Sula nebouxii*) that maintained their pair bond establish clutches earlier, have a higher hatching success and produce more fledglings than those birds with unfamiliar mates (Sanchez-Macouzet et al. 2014). Thus, maintaining stable pair bonds seems a crucial strategy for maximising immediate reproductive success in seabirds.

### Short foraging trip duration increases fledging success, but reduces hatching success

The little penguin population had a higher proportion of fledging success in years with shorter average foraging trip durations, while longer foraging trips increased the proportion of hatching success. Previous studies have shown that shorter foraging trips are correlated with higher fledging success in little penguins and that they are likely associated with good foraging conditions, which permit parents to get food for their chicks more quickly (Chiaradia and Nisbet 2006; Saraux et al. 2011b). These findings are consistent with studies on seabirds in general, where poorer foraging opportunities increase time spent away from chicks, with smaller meal sizes and less frequent meal delivery to chicks resulting in lower reproductive success (Weimerskirch et al. 1997; Chivers et al. 2012; Boersma and Rebstock 2009). Alternatively, during the egg incubation phase, we found that longer foraging trips were associated with increased proportions of hatched eggs within the population. This result contrasts with other studies in poor breeding seasons when longer foraging trips were associated with lower hatching success (Chiaradia and Kerry 1999; Kemp and Dann 2001). If the incubating partner is left a long time to incubate, they may be forced to abandon the nest due to depleted fat stores (Olsson 1997). However, little penguins in this population spent as long as nine days on foraging trips and still successfully hatched eggs (Kato et al 2008) and the longest average foraging trip duration observed in this study was 2.2 days, which is well within the limits that fat stores last in this species (Gales and Green 1990). This suggests food may not have been a limiting factor for adults during the study period. Therefore, while foraging trip duration is an important factor mediating success in chick-rearing, it is not generally a strong factor in incubation.

### Environmental conditions

Marine environmental conditions were not strong predictors of little penguins' reproductive success in this study. While marine environmental conditions affect food availability and foraging conditions that affect the reproductive outcome (Kowalczyk et al. 2015, Saraux et al. 2011b, 2016), these conditions were less important when environmental and behavioural factors were analysed together. These findings were unexpected. Little penguins have responded strongly to changes in environmental conditions in previous studies, such as shortened foraging trip durations during La Niña (Berlincourt and Arnould 2015), leading to higher reproductive success (Chiaradia and Nisbet 2006). SST also affects reproductive success of other seabirds (Chambers 2004; Becker et al. 2007; Erwin and Congdon 2007). However, SST should be used with caution, as it can produce conflicting results at different stages of the breeding (Afán et al 2015). In one population, warmer SST in months before breeding led to more chicks and larger fledglings (Cullen et al. 2009), whereas in another population, the opposite was found (Cannell et al 2012). Little penguins may be able to mitigate the consequences of variable environmental conditions by using flexible behaviours. Seabirds exhibit plasticity in their foraging strategies, whereby they alter their foraging spatially, temporally and, in some cases, target different prey species to buffer the effects of unpredictable prey availability (Burke and Montevecchi 2009; Garthe et al. 2011). Combining environmental and behavioural parameters revealed the intricate interplay of factors affecting breeding success. This holistic approach underscores the complexity of reproductive ecology and highlights the importance of considering multiple factors to accurately understand and predict breeding outcomes.

### Conclusions

Our comprehensive study of the little penguin breeding colony over 13 breeding seasons provides a clearer understanding of the interplay between social behaviour and indices that influence reproductive success. Notably, divorce rate emerged as the most reliable predictor, with lower divorce rates correlating with higher hatching and fledging success. Shorter foraging trips were found to benefit prospects of fledging success but shorter foraging trip durations during incubations increased hatching success, suggesting complex dynamics between foraging behaviour and reproductive stages. Contrary to our expectations, marine environmental conditions did not strongly predict reproductive success once analysed concurrently with social and behavioural aspects. This is possibly due to the penguins' behavioural flexibility in adapting to varying conditions. Our study underscores the importance of social factors, particularly pair stability, in reproductive outcomes. Monitoring divorce rates could be a valuable tool for predicting and managing the reproductive success of little penguin populations. It can add significant value to conservation efforts, potentially guiding broader conservation strategies across different species in marine environments.

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**Table 1** Spearman correlations between behavioural and environmental parameters measured at a little penguin colony at Phillip Island, Australia (n = 12 breeding seasons). \*\*\* = < 0.001, \* = < 0.05

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Correlations** | | | |
| **Parameter** | **1.** | **2.** | **3.** | **4.** |
| 1. Divorce rate |  |  |  |  |
| 2. Foraging trip duration (days) | 0.15 |  |  |  |
| 3. Delta temperature (Δ T) | 0.69\* | -0.12 |  |  |
| 4. SST | -0.69\* | 0.08 | -0.91\*\*\* |  |
| 5. SOI | -0.30 | -0.05 | -0.12 | 0.22 |

**Table 2** Effect size estimate, standard error and confidence intervals produced by model averaging of environmental and behavioural predictor variables on the average number of eggs produced per pair in little penguins at Phillip Island, Australia (N = 12 breeding seasons).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Parameter | Estimate | Unconditional SE | Confidence interval | Relative importance |
| *Intercept* | 1.873 | 0.269 | (1.345, 2.400) |  |
| Divorce rate | -0.302 | 0.211 | (-0.716, 0.113) | 0.30 |
| Foraging trip duration (days) | 0.180 | 0.160 | (-0.177, 0.537) | 0.15 |
| SOI | 0.002 | 0.003 | (-0.004, 0.008) | 0.14 |
| SST | 0.022 | 0.035 | (-0.056, 0.099) | 0.08 |

**Table 3** Effect size estimate, standard error and confidence intervals produced by model averaging of environmental and behavioural predicator variables on proportion of hatching success in little penguins at Phillip Island, Australia (N = 12 breeding seasons).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Parameter | Estimate | Unconditional SE | Confidence interval | Relative importance |
| *Intercept* | 0.187 | 2.383 | (-4.484, 4.859) |  |
| Divorce rate | -4.284 | 1.052 | (-6.345, -2.223) | 1.00 |
| Foraging trip duration (days) | 1.674 | 0.669 | (0.362, 2.986) | 0.92 |
| SOI | -0.020 | 0.009 | (-0.039, -0.002) | 0.78 |
| SST | -0.312 | 0.207 | (-0.717, 0.093) | 0.13 |

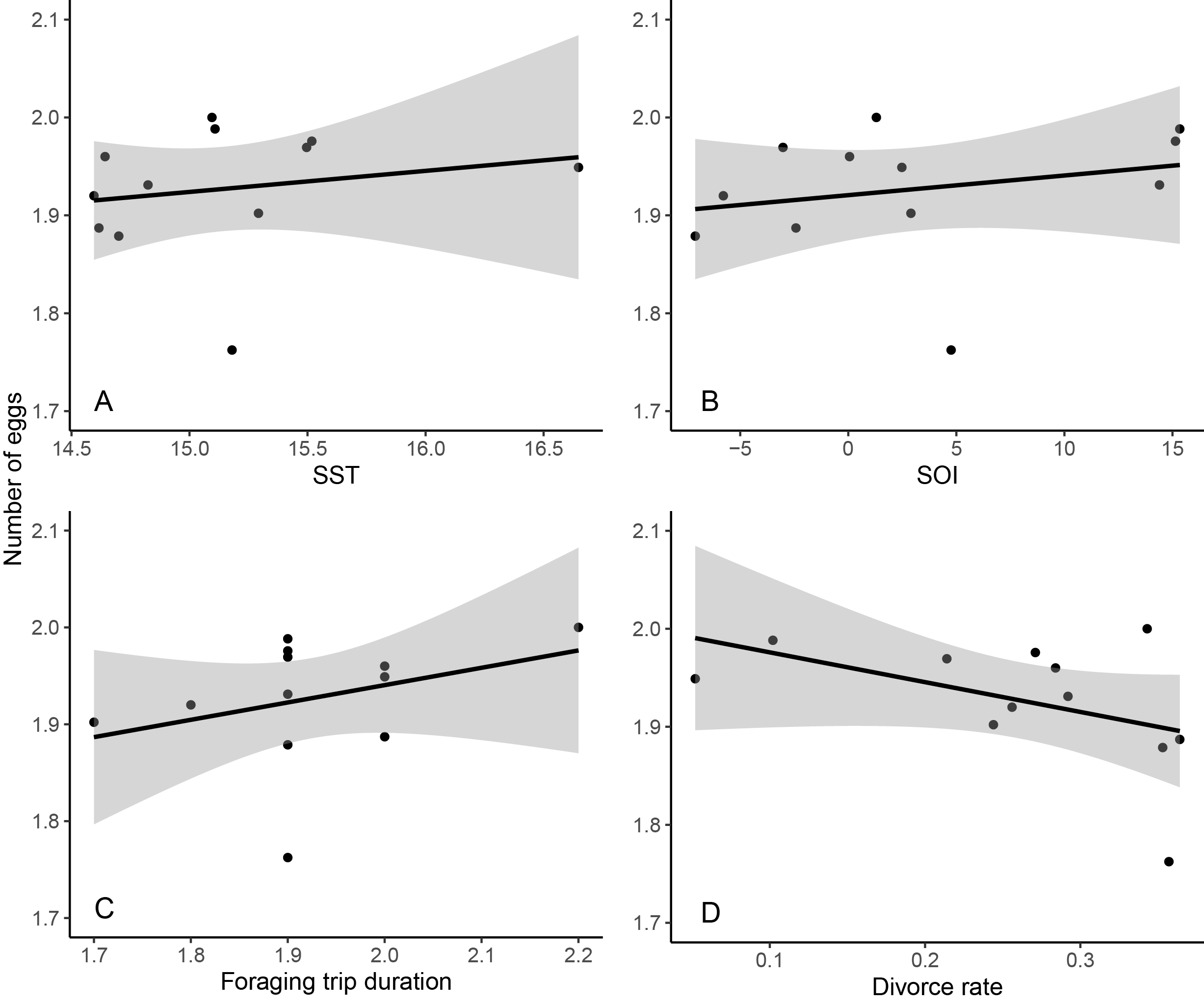
**Table 4** Effect size estimate, standard error and confidence intervals produced by model averaging of environmental and behavioural predictor variables on proportion of fledging success in little penguins at Phillip Island, Australia (N = 12 breeding seasons).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Parameter | Estimate | Unconditional SE | Confidence interval | Relative importance |
| *Intercept* | 8.508 | 1.644 | (5.286, 11.730) |  |
| Divorce rate | -3.707 | 0.790 | (-5.256, -2.159) | 1.00 |
| Foraging trip duration (days) | -3.616 | 0.689 | (-4.966, -2.266) | 1.00 |
| SOI | -0.032 | 0.009 | (-0.051, -0.015) | 1.00 |
| SST | 0.173 | 0.184 | (-0.188, 0.534) | 0.08 |

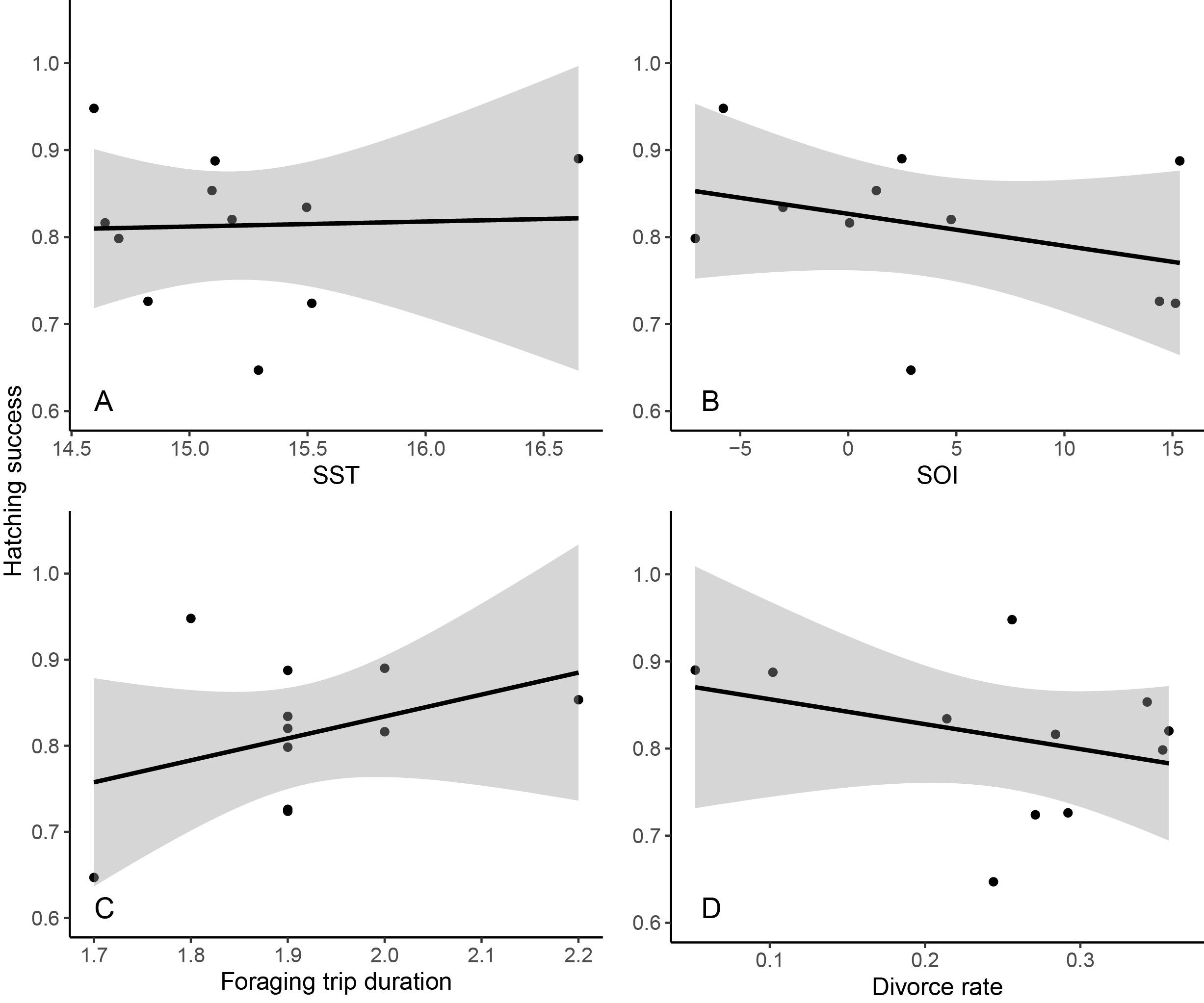
**Table 5** Effect size estimate, standard error and confidence intervals produced by model averaging of environmental and behavioural predictor variables on the average number of fledglings produced per pair in little penguins at Phillip Island, Australia (N = 12 breeding seasons).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Parameter | Estimate | Unconditional SE | Confidence interval | Relative importance |
| *Intercept* | 1.660 | 1.795 | (-1.859, 5.179) |  |
| Divorce rate | -1.986 | 1.067 | (-4.077, 0.105) | 0.57 |
| Foraging trip duration (days) | -1.038 | 0.876 | (-2.754, 0.679) | 0.21 |
| SOI | -0.012 | 0.014 | (-0.010, 0.015) | 0.14 |
| SST | 0.051 | 0.262 | (-0.462, 0.565) | 0.12 |

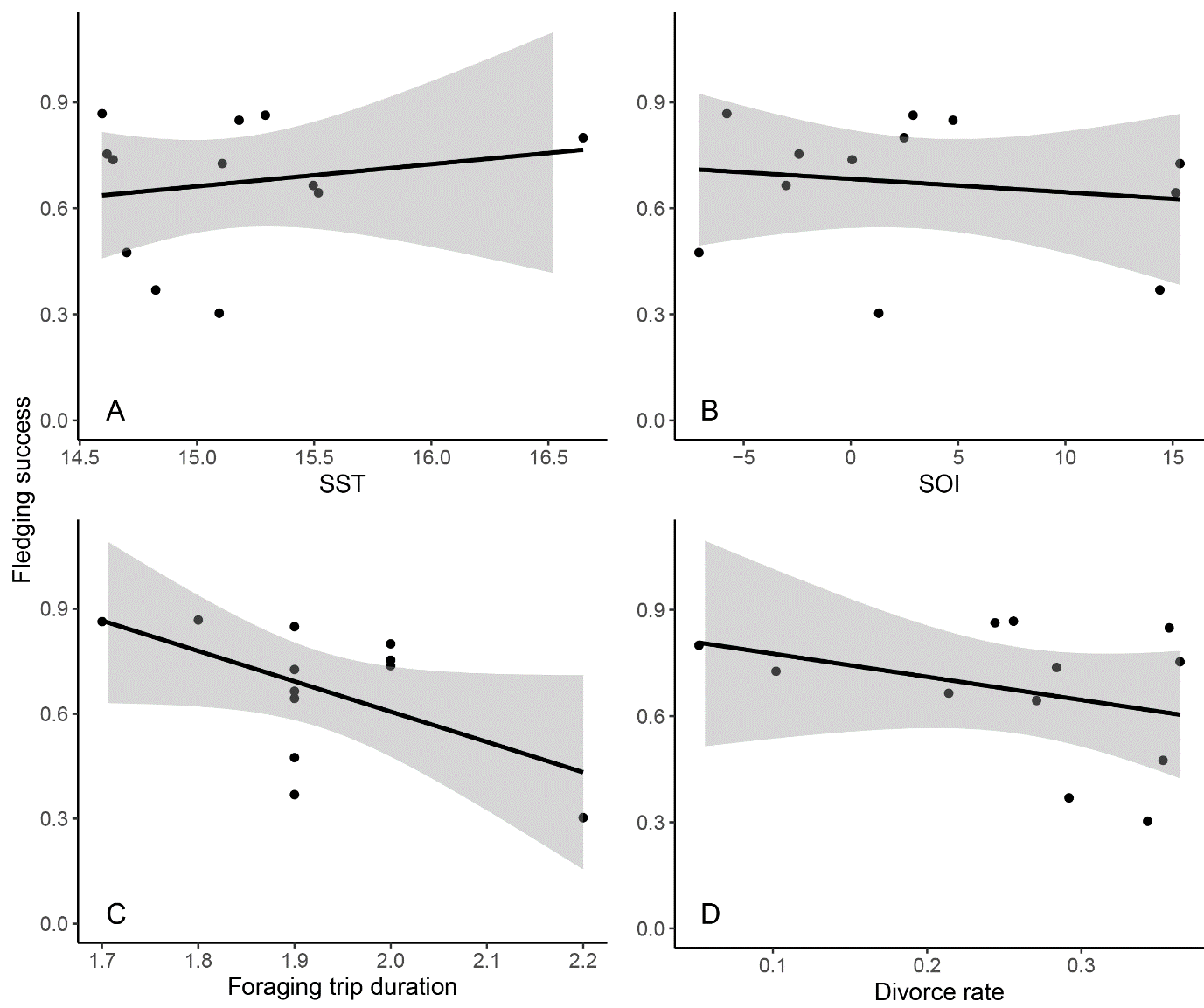
**Figures**



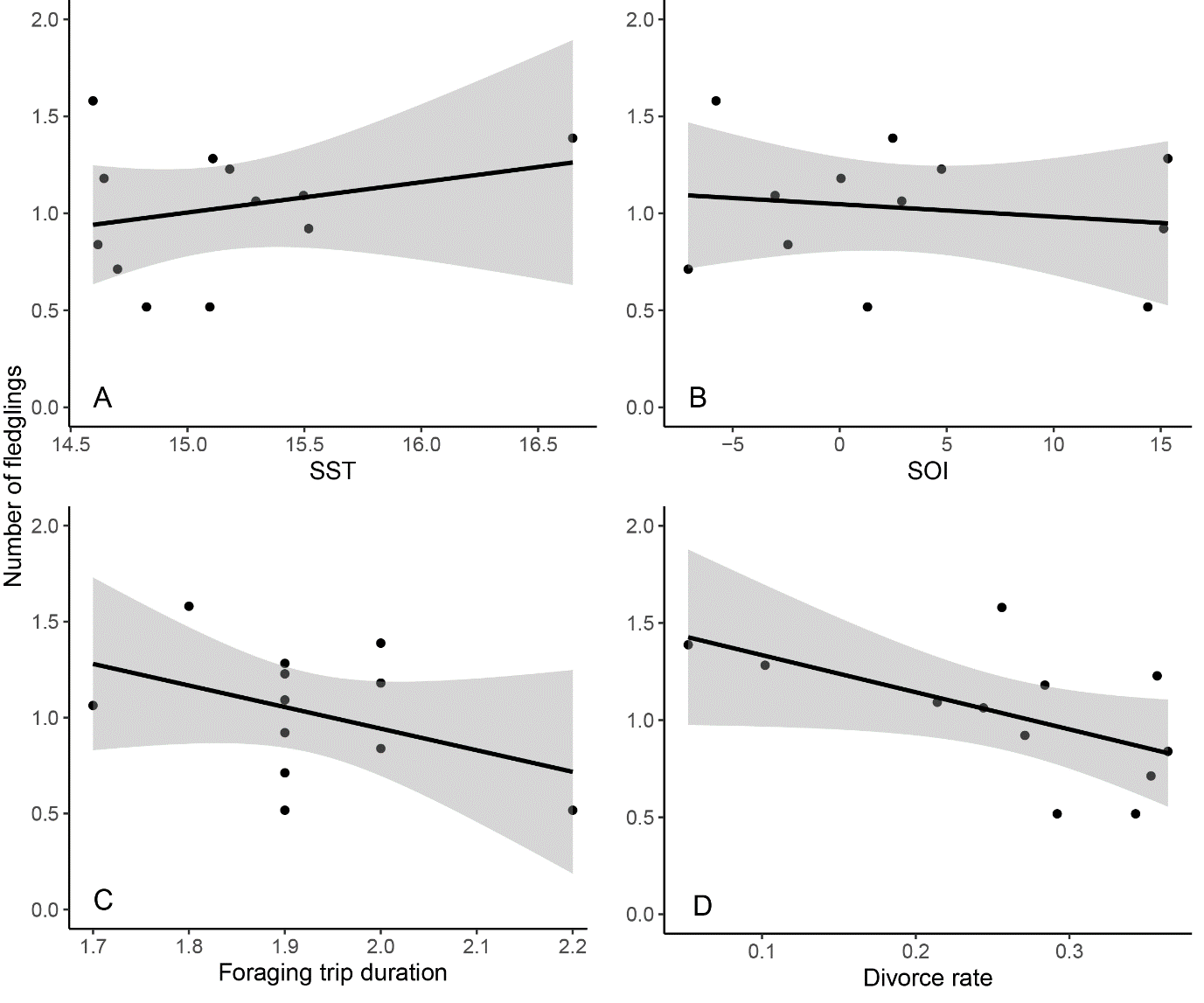
**Figure 1** Average number of eggs laid by pairs each breeding season (2001 – 2012) in a population of little penguins, at Phillip Island, Australia, against predictor variables a) SST, b) SOI, c) foraging trip duration (days) and d) divorce rate.



**Figure 2** Hatching success (proportion of hatched eggs by number of eggs laid) each breeding season (2001 – 2012) in a population of little penguins, at Phillip Island, Australia, against predictor variables a) SST, b) SOI, c) foraging trip duration (days) and d) divorce rate.

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**Figure 3** Fledging success (proportion of fledged chicks by number of chicks hatched) each breeding season (2001 – 2012) in a population of little penguins, at Phillip Island, Australia, against predictor variables a) SST, b) SOI, c) foraging trip duration (days) and d) divorce rate.



**Figure 4** Average number of fledglings by pairs each breeding season (2001 – 2012) in a population of little penguins, at Phillip Island, Australia, against predictor variables a) SST, b) SOI, c) foraging trip duration (days) and d) divorce rate.