Breeding behaviour and success of the Tasmanian wedge-tailed eagle

(Aquila audax fleayi)

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Declaration

I hereby declare that this thesis contains no material which has previously been accepted for the award of any other degree or diploma and contains no copy or paraphrase of material previously published or written by any other person, except where due reference is made in the text of this thesis.

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26th May 2014

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Abstract
Vertebrate predators, and raptors in particular, are of high conservation concern. However, despite their high ecological importance, there is a paucity of knowledge of many raptor species, including the threatened Tasmanian wedge-tailed eagle, *Aquila audax fleayi*. The Tasmanian wedge-tailed eagle is sensitive to disturbance during the breeding season, which has been qualitatively linked to breeding failure. Breeding success is a product of breeding timing and behaviour on the nest, as well as biotic and abiotic environmental factors. This study aimed to establish the critical abiotic and biotic factors that influence the timing and success of breeding pairs throughout Tasmania. On an individual level, it aimed to determine which behaviours wedge-tailed eagles exhibit on their nest, how they respond to disturbance, and whether their responses indicate habituation or sensitisation over time. Mixed effects modelling techniques were employed to examine the impact of several candidate environmental factors, including climate, prey availability, road density and nest density, on breeding success and timing. Breeding success data was obtained from aerial surveys conducted by the Forest Practices Authority (2007-present). Breeding success was negatively associated with spring rainfall and nest density, while no significant association was found with other variables (prey, temperature, and road density). Colder winters and increased spring rainfall corresponded to later breeding times, while prey availability did not have a significant impact. Behavioural responses to pedestrian disturbance observed at 12 nests during this study supported the hypothesis that wedge-tailed eagles are extremely sensitive to disturbance, with flushing off the nest a common response to the observers’ approach. The behavioural responses to the approach worsened over time, providing evidence for a tendency to sensitise to repeated disturbance. This sensitivity was confirmed by the high levels of nest failure within the study nests (2 successful, 10 failed). Overall, this study identifies a number of interacting variables which can limit wedge-tailed eagle reproduction. On a population level, rainfall, cold temperatures, and nest density are associated with not only lower breeding success in Tasmanian wedge-tailed eagles, but also delays in the timing of the breeding season. On an individual scale, human disturbance alters breeding behaviour, and responses to disturbance (i.e. flushing) can leave chicks or eggs exposed to the elements or predation, thus increasing the likelihood of nest failure.
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1. Introduction

Vertebrate predators are of special concern for biodiversity conservation (Gittleman et al. 2001; Sergio et al. 2006; Letnic & Koch 2010). They play a regulatory role in maintaining ecosystem structure and function, as evidenced by widespread and dramatic shifts following the declines of predators in marine, terrestrial, and freshwater ecosystems worldwide (Schmitz, Hamback & Beckerman 2000; Smith, Peterson & Houston 2003; Finke & Denno 2004; Estes et al. 2011). Furthermore, predators have intrinsic properties that make them more vulnerable than other species, and they are threatened at a disproportionate rate, with recent mass extinctions characterised by apex predators (Ray et al. 2005; Estes et al. 2011). Predators face threats that affect most animals, including habitat loss and disease (Butler 2004; McCallum 2008; Forero-Medina et al. 2009), but also additional threats, including vulnerability due to naturally low population densities stemming from a need for expansive foraging territories (Gittleman & Harvey 1982; Grant, Chapman & Richardson 1992). As a result of their wide-ranging nature and real or perceived conflict with humans and domestic animals, predators can also be a target of human persecution (Treves & Karanth 2003; Graham, Beckerman & Thirgood 2005; Ogada & Keesing 2010; Ahmed et al. 2012).

Raptors, as predatory birds, face similar challenges to other predators, including intrinsically low population densities (Schoener 1969), persecution (Green et al. 2004; Thiollay 2006) and disease (Schettler et al. 2003; Ellis et al. 2007), as well as special challenges such as bioaccumulation of toxins (Dykstra et al. 1998; Pain et al. 2005; Perez-Lopez et al. 2008), and collision with anthropogenic structures (Sergio et al. 2004; Tapia, Dominguez & Rodriguez 2009; Dahl et al. 2012; Hull et al. 2013). Raptors are threatened at a higher rate than non-predatory bird species: 17.3% of Falconiformes and Strigiformes species are listed as threatened, compared to 12.8% of all other bird species (IUCN 2013). To aid their conservation, numerous management efforts have been put in place to help protect raptor species worldwide (McCollough, Todd & Owen 1994; Bell & Mooney 1999; Lehman, Kennedy & Savidge 2007). However, these efforts are costly, and their effectiveness is dependent on the scientific research available, so ongoing research and monitoring is essential for improving the efficacy of these campaigns.
Despite the ecological importance of raptors as apex predators (Sergio et al. 2006), and the high proportion of species that are threatened, there is a paucity of basic knowledge of many raptor species (Bamford et al. 2007; Whitfield, Ruddock & Bullman 2008). Many raptor species are intrinsically difficult to study due to low population densities, high agility, and avoidance of humans, so much of our knowledge of raptors is based on expert opinion (Whitfield, Ruddock & Bullman 2008). Of the research conducted on raptors, breeding success has been a primary focus, as nests are easier to study than highly agile birds (Newton 1979). Raptors have intrinsically low reproductive rates due to a number of life history traits (e.g. small clutch sizes, protracted nest dependence of offspring, and late sexual maturity; Amadon 1964), and low reproductive rates contribute to population decline in species of conservation concern (Dykstra et al. 1998; González et al. 2006b).

Reproductive rates typically vary between years (Steenhof & Newton 2007), and depending on the measure of breeding success, observed breeding performance can be influenced by territory occupancy (Sergio & Newton 2003), probability of birds nesting within each territory, the nesting success of individual breeding pairs, and fledgling survival (McIntyre & Schmidt 2012). Different studies often utilize different measures, so comparing breeding performance between species is not necessarily accurate, particularly in species with supernumerary nests (Steenhof & Newton 2007).

The timing of the breeding season and breeding behaviour are both adapted to increase the likelihood of breeding success while minimising costs to adults, particularly in long-lived raptor species (Hanssen et al. 2005; Shawkey et al. 2009; D’Alba, Oborn & Shawkey 2010). Thus, alterations to the timing or behavioural patterns of breeding can impact breeding success (Bart & Tornes 1989; Samelius & Alisauskas 2001; Duncan Rastogi, Zanette & Clinchy 2006; Verhulst & Nilsson 2008). The timing of a bird’s breeding season, typically defined as the laying date, or start date of incubation (Steenhof & Newton 2007), has been shown to affect nest success, in that early breeders tend to produce more numerous and higher quality young (Gargett 1977; Krüger 2004; Steenhof & Newton 2007; Verhulst & Nilsson 2008; Koch, Martin & Aitken 2012). There are strong impacts of breeding behaviour on timing and success, as higher nest attendance is correlated with higher breeding success (Samelius & Alisauskas 2001) and shorter incubation periods (Wiebe, Wiehn & Korpimäki 1998). Though breeding timing
and behaviour are highly adapted, they can exhibit plasticity, and can vary based on changes in intrinsic and extrinsic, biotic and abiotic factors.

Breeding success is linked to a number of biotic and abiotic factors that influence breeding on both an individual and population level. Factors that commonly influence breeding in raptors include bird age (Penteriani, Balbontin & Ferrer 2003), weather (Gargett, Gargett & Damania 1995; Steenhof, Kochert & McDonald 1997; Steidl, Kozie & Anthony 1997; Krüger 2004), prey availability (Dykstra et al. 1998; Martin et al. 2009; Whitfield et al. 2009; McIntyre & Schmidt 2012), individual characteristics of the breeding pair (e.g. plumage morph) (Krüger 2004), nest characteristics (Radford & Plessis 2003; Jiménez-Franco, Martínez & Calvo 2014), and human influence (Holtthuijzen et al. 1990; Kaisanlahti-Jokimäki et al. 2008; Lambertucci & Speziale 2009). The degree to which these variables influence breeding success, timing, and behaviour is often species and habitat specific (Kostrzewa & Kostrzewa 1990; Olsen & Olsen 1992).

Weather, particularly temperature and rainfall extremes, can affect breeding success, timing and behaviour. Species that breed at high latitudes tend to rely on photic cues and thus have highly synchronous breeding seasons (Garamszegi et al. 2008), while birds at lower latitudes tend to have longer and more variable breeding seasons with increasing reliance on weather cues (Zann et al. 1995; MacDougall-Shackleton & Hahn 2007). Temperature is a cue for many birds to begin breeding (Visser, Holleman & Caro 2009), with warm temperatures leading to an early onset of incubation (Ardia, Cooper & Dhont 2006). Colder temperatures during the winter and spring relate to later breeding times and a lower proportion of egg-laying pairs of golden eagles, *Aquila chrysaetos*, in North America (Steenhof, Kochert & McDonald 1997). The onset and success of the breeding season can be dependent on rainfall (Zann et al. 1995; Lloyd 1999), particularly in arid environments, where higher rainfall corresponds to higher prey abundance (Ridpath & Brooker 1985; Gargett, Gargett & Damania 1995). However, in areas with higher average rainfall, inclement weather conditions prior to and during incubation and brood rearing stages can reduce hunting efficiency and be detrimental to offspring survival (Gargett 1977; Hustler & Howells 1986; Kostrzewa & Kostrzewa 1990; Radford & Plessis 2003; Bionda & Brambilla 2012). Weather can also
influence breeding behaviour, with higher nest attentiveness in adverse conditions, and reduced risk of flushing when disturbed (Beer 1961; Steidl & Anthony 2000).

Prey availability also plays a role in determining the onset of incubation and breeding success of many raptors, particularly in species with specialised diets (Hanski, Hansson & Henttonen 1991; Gargett, Gargett & Damania 1995; Wiebe, Korpimäki & Wiehn 1998). Reproduction comes at a high energy cost to breeding birds, and requires a substantial allocation of nutrients, which must be either internally drawn from body reserves or obtained externally from food resources at the onset of and during breeding (Jones & Ward 1976; Krapu 1981; Wiebe, Wiehn & Korpimäki 1998). Thus, it is expected that higher prey populations correspond to earlier breeding attempts (Kostrzewa & Kostrzewa 1990; Steenhof, Kochert & McDonald 1997) and more consistent breeding timing between individuals (Ridpath & Brooker 1985). Since generalist raptor species can supplement their diet from a number of prey species (Harder 2000; Ontiveros & Plegueznel 2000), the impact of prey availability on breeding is greater in areas where prey is a limiting resource for raptors (González et al. 2006b; McIntyre & Schmidt 2012). If prey is a limiting resource, its availability can impact breeding success in two ways: 1) low prey abundance prior to the breeding season can result in fewer pairs laying eggs, likely due to a minimum body condition required prior to incubation (Jones & Ward 1976; Steenhof, Kochert & McDonald 1997); and 2) low prey availability during the breeding season could reduce the likelihood of breeding success, with adults requiring more time for foraging to maintain their own condition and provide for nestlings (Steenhof, Kochert & McDonald 1997; Salamolard et al. 2000; González et al. 2006b). Prey availability may also influence breeding behaviour, as some raptors exhibit lower nest attentiveness (Wiebe, Wiehn & Korpimäki 1998; Dewey & Kennedy 2001), or are less tolerant to human disturbance during periods of food stress (Van der Zande & Verstrael 1985; White & Thurow 1985).

Human activities can significantly influence raptor breeding success and behaviour, and in a small number of studies have been linked to the timing of the breeding season (Millsap et al. 2004). Some raptor species respond positively to human-altered environments, and have enhanced breeding performance in suburban and urban habitats (Chace & Walsh 2006; Stout, Temple & Papp 2006). However, the majority of raptor species are more sensitive to human disturbance and exhibit lower breeding success in
areas with greater human presence (Krüger 2004). Human disturbance occurs in a number of ways, including direct disturbance that reduces habitat physically (e.g. logging), or indirect disturbances which are non-consumptive activities (e.g. recreation, traffic) that temporarily exclude animals from optimal habitats or alter behaviours required for survival and reproduction (Steidl & Anthony 2000). Even scientific methods of checking nests for activity can have a negative influence on breeding success (Grier 1969; Westmoreland & Best 1985; Gotmark 1992; Carney & Sydeman 1999).

Human disturbance can affect the breeding behaviour of raptors in both subtle and overt ways, with corresponding impacts on their reproduction (Steidl & Anthony 2000). A number of studies have examined breeding behaviour of raptors (Levenson 1979; Bollen 1991; Bryan et al. 2005), and the response of raptors to disturbance outside of the breeding season (Stalmaster & Newman 1978; Holmes et al. 1993; Stalmaster & Kaiser 1997). However, the majority of studies examining breeding success do not take behaviour into account, leaving a gap in knowledge of how behaviour can influence nest success (Steenhof & Newton 2007). Substantial disturbance can cause adults to abandon nests, or flush off nests temporarily (Mooney & Holdsworth 1991; Whitfield et al. 2003). Flushing is the most common ‘disturbed’ behaviour reported (Grubb & King 1991; Richardson & Miller 1997) and can have detrimental effects on chick health, ranging from periodic cooling resulting in prolonged incubation periods (Lyon & Montgomerie 1985; Nilsson & Henrik 1988), reduced immunity and body condition of nestlings (Ardia, Perez & Clotfelter 2010), to nest failure due to embryonic death or nest predation (Martin et al. 2007). Prolonged incubations can result in later hatch dates and thus disadvantage breeding adults as well as chicks. As incubation is associated with high energetic costs for breeding adults, prolonged incubation could result in lower future fecundity as it has been linked to reduced immune function and weight loss in long-lived bird species (Hanssen et al. 2005). Prolonged incubation also has negative impacts on chicks by reducing time available for acquiring flying and foraging skills before winter when daylight hours are shorter and conditions are less favourable, thus reducing offspring fitness (Martin 1987). Minor disturbances can induce more subtle behavioural or physiological changes that may lower adult fitness, but these subtle
changes are much harder to detect and thus have less of a presence in the literature (White & Thurow 1985; González et al. 2006a).

Nest switching, or the use of alternative nests in subsequent breeding seasons, is a behaviour that has long been associated as a response to disturbance, but recent findings suggest that it may have other foundations. Nest reuse is lower in territories with more alternative nests (Saga & Selás 2012). Switching between alternative nests in a territory can increase breeding success by reducing the prevalence of ectoparasites on nests (Ontiveros, Caro & Pleguezuelos 2008b; Ontiveros, Caro & Pleguezuelos 2008a). Switching may also be necessary if a nest is usurped by competitors (Ontiveros, Caro & Pleguezuelos 2008b). Nest switching and the subsequent high number of alternative nests has also been hypothesised to increase with nest failure (Brown 1976; Newton 1979), particularly following disturbance events (De Santo et al. 2002; Saga & Selás 2012). However, the link between alternative nests and disturbance has remained largely untested and recent studies of eagle nests have not supported the hypothesis (Ontiveros, Caro & Pleguezuelos 2008b; Kochert & Steenhof 2012).

Sensitivity to disturbance is variable in eagles, possibly indicating habituation to repeated disturbance in tolerant breeding pairs, particularly if pairs nest successfully in areas with consistent human activity (Knight 1995; Richardson & Miller 1997). However, there are few studies that experimentally test whether eagles habituate or sensitise to disturbance (Steidl & Anthony 2000). Steidl and Anthony (2000) found evidence for habituation of bald eagles, *Haliaeetus leucocephalus*, to disturbances lasting for prolonged periods of time, whereupon their behaviour tended to resemble the behaviour found at undisturbed nests. However, the number of vocalisations, which was significantly higher in disturbed nests than controls, did not decrease over the length of the disturbance, suggesting that birds were still disturbed even though most of their behaviours approached those of undisturbed nests.

Classification of individuals or species as tolerant to disturbance based solely on single observations of behavioural responses to disturbances is insufficient. Perceived tolerance or habituation to human activities can be misleading, as disturbed animals can respond in non-behavioural ways: physiologically (e.g. higher levels of stress hormones, or glucocorticoids) (Culik, Adelung & Woakes 1990), or facing long term declines in fitness (Millsap *et al.* 2004). A recent study conducted by Strasser and Heath (2013)
examining the effects of anthropogenic disturbance on a ‘tolerant’ raptor species, the European kestrel (*Falco tinnunculus*), found that proximity to human development was common, but was associated with higher levels of glucocorticoids and nest abandonment. Bald eagles have also been described as tolerant to human disturbance, with nests in suburban areas often producing chicks (*Nesbitt 2001; Millsap et al. 2004*). However, recent findings show that the chicks from suburban nests have significantly reduced survival within a year of fledging compared to chicks from more rural areas (*Millsap et al. 2004*). Thus, the apparent tolerance of anthropogenic activities by some species or individuals may not necessarily be the case and these animals may be in an ecological trap, which is typified by animals selecting low quality and often human-modified habitat (*Gill, Norris & Sutherland 2001; Battin 2004*). Behavioural studies coupled with longitudinal studies on fitness or reproductive output can provide evidence for the true costs of human disturbance to fitness or reproductive ability.

**Study species**

The Tasmanian wedge-tailed eagle, *Aquila audax fleayi*, is one of Tasmania’s few remaining apex predators. Of the island state’s four large marsupial carnivores, one (the thylacine, *Thylacinus cynocephalus*) is extinct and two are listed as threatened (the spotted-tailed quoll, *Dasyurus maculatus*, and the Tasmanian devil, *Sarcophilus harrisii*) (*State Government of Tasmania 1995; McCallum & Jones 2006; Byholm & Kekkonen 2008*). The other avian apex predator, the white-bellied sea eagle (*Haliaeetus leucogaster*) is also listed as threatened in Tasmania (*State Government of Tasmania 1995*) and has a more confined distribution than *A. a. fleayi*, as it tends to nest close to coastal areas and inland lakes (*Thurstans 2009*).

The Tasmanian wedge-tailed eagle has been classified as a separate subspecies of the wedge-tailed eagle present on the mainland of Australia, *Aquila audax audax*. Mainland adults have darker plumages (*Bell & Mooney 1999*); while Tasmanian adults have a larger body size (*Nankervis 2010*), are obligate tree nesters with smaller clutch sizes (*Brown & Mooney 1997*), and exhibit higher sensitivity during the breeding season (*Mooney & Holdsworth 1991*). However, recent genetic research has suggested that the divergence between the mainland population and the Tasmanian population is relatively
recent and that phenotypic differences may be due to strong influences of founding individuals (Burridge et al. 2013).

The Tasmanian subspecies is listed as threatened on both a state and federal level (State Government of Tasmania 1995; Commonwealth of Australia 1999). Principal threats include loss of nesting habitat, disturbance of nesting birds, collision with man-made structures, and persecution; though persecution by humans is becoming less prevalent (Starker Leopold & Wolfe 1970; Gaffney & Mooney 1992). The high sensitivity to disturbance at nest sites has been documented for decades, and human activities near nests have been linked to nest failures and nest abandonments (Mooney & Holdsworth 1991; Gaffney & Mooney 1992; Mooney & Taylor 1996), but the majority of reports have been qualitative. Breeding pairs exhibit significant variation in their tolerance to humans, with examples of tolerant pairs breeding successfully in suburban areas (Harder 2000). The mechanism for the increased tolerance (e.g. via genetic factors or habituation) is unknown.

The Tasmanian wedge-tailed eagle has relatively specific breeding habitat requirements, with nests primarily found in emergent trees in sheltered patches of old-growth native forest (Brown & Mooney 1997). Foraging requirements are much less specific. Tasmanian wedge-tailed eagles are generalists and opportunistic predators and can forage capably over most types of terrestrial habitat (Gaffney & Mooney 1992). On the mainland of Australia A. a. audax diets vary regionally, with the predominant prey species of rabbits and hares, birds, kangaroos, or reptiles, depending on the habitat in question (Starker Leopold & Wolfe 1970; Brooker & Ridpath 1980; Ridpath & Brooker 1985; Harder 2000; Collins & Croft 2007). The diet of the Tasmanian wedge-tailed eagle is similarly varied and is comprised of both live prey and carrion. Known prey species include rabbits, hares, cats, wallabies, possums, echidnas, wombats, birds, sheep, goats, and reptiles (Gaffney & Mooney 1992).

The ecological importance of the wedge-tailed eagle in Tasmania, coupled with its endangered status, has resulted in measures to aid in the conservation of this subspecies. Environmental regulators impose significant constraints on human and industry activities around eagle nests (FPA 2012). Current management prescriptions carried out in areas covered by the Forest Practices System include pre-harvest surveys for nests, establishment of reserves around known nests (minimum 10 ha), and restrictions on
activities within 500 m or 1 km line-of-sight of active nests during the breeding season (FPA 2012). Similar conditions are generally required by other state government regulators for activities including quarrying, dam works, mining, and other developments (C. Hawkins, pers. comm.). As there are over 1,400 known Tasmanian wedge-tailed eagle nests (DPIPWE 2013), and the breeding season restrictions occur from July to January or February, the management implications of eagle nest avoidance are costly for a dominant sector of Tasmanian industry.

Understanding the factors driving the observed variation in breeding success and timing of the Tasmanian wedge-tailed eagle could help guide future management. Ongoing nest surveys indicate that the timing of the breeding season and overall nest success varies between years and individual nests, and that earlier breeding seasons may correspond to higher breeding performance (Koch, Wiersma & Munks 2012). However, reasons for the annual and inter-individual variation in nest success and breeding timing of the Tasmanian wedge-tailed eagle are unknown.

The limited knowledge of the Tasmanian wedge-tailed eagle, combined with its endangered status and costly management provisions, call for a greater understanding of its ecology, particularly during the breeding season when it is most sensitive. Much of the knowledge of the breeding behaviour and impacts of disturbance on the Tasmanian wedge-tailed eagle is based on expert opinion and limited quantitative data, or extrapolated knowledge from the mainland subspecies. Though expert opinion can be a valuable and realistic resource, its use should be temporary until more empirical data are gathered (Whitfield, Ruddock & Bullman 2008). Additionally, since Tasmania differs from the mainland in a number of characteristics including vegetation, climate, and species composition, and the Tasmanian wedge-tailed eagle is phenotypically different from the mainland subspecies in many ways (Burridge et al. 2013), extrapolating knowledge about the mainland subspecies to the lesser-studied Tasmanian subspecies is not necessarily accurate.

**Study aims**

The timing of the breeding season, breeding success, and breeding behaviour are all interrelated factors influencing both adult and chick fitness in the short-term, and population dynamics over the long-term, so understanding these factors is likely to be
essential to the conservation of any raptor species. In this study, I examined the breeding success of the Tasmanian wedge-tailed eagle on two scales. On a population scale, I examined possible explanations for the variation in the timing of the breeding season and breeding success of a large sample of Tasmanian wedge-tailed eagle nests over multiple breeding seasons. On an individual scale, I investigated breeding behaviour and breeding success through intensive behavioural surveys on a subset of Tasmanian wedge-tailed eagle nests. I incorporated these two approaches to address the following aims:

1. *Timing of the breeding season:* Determine if weather and prey influence the timing of the breeding season in the Tasmanian wedge-tailed eagle.

2. *Breeding success:* Estimate the level of nest failure state-wide, and test the impact of weather, prey, and disturbance variables on the likelihood of nest success in the Tasmanian wedge-tailed eagle.

3. *Breeding behaviour:* Determine the breeding behaviour of individual breeding pairs, their behavioural responses to disturbance, and test whether their responses to repeated disturbance indicate habituation or sensitisation over time.

Due to the variability in the climate of Tasmania, particularly with high rainfall in the winter and spring, I hypothesised that colder, wetter weather prior to the breeding season would correspond to delays in the onset of incubation and lower breeding success. Since the Tasmanian wedge-tailed eagle is a generalist predator, I expected only a weak relationship with prey abundance, but that greater prey abundance would correspond to earlier and more successful breeding seasons. I also hypothesised that human activity would correspond to lower nest success by altering adult behaviour and increasing the likelihood of nest failure. However, due to the incidence of ‘tolerant’ breeding pairs I expected that breeding birds habituate and behavioural responses to repeated disturbance would lessen over time.
2. Methods

Study area
Nests included in the study are distributed across both public and private lands throughout the island of Tasmania, Australia, which is located 240 km south of the mainland of Australia (Figure 1). With an area of 68,401 km$^2$, Tasmania is centred at approximately 42° S, 147° E. Tasmania’s temperate maritime climate is characterised by mild summers, and cool wet winters. Due to variation in elevation (0 – 1,617 m), geology, and climate throughout the state, Tasmania’s vegetation is defined by a complex mosaic of communities ranging from button grass moorland to wet sclerophyll forests (Williams 2012).

Data collection

Breeding timing
The timing of the breeding season, (i.e. the start date of incubation) was estimated using data on chicks of known age, and extrapolated using information on the timing of the different stages of breeding (Koch, Wiersma & Munks 2012). Nestlings were aged from two sources: direct observations during aerial surveys conducted by the FPA (see below for details), and photographs submitted by forest planners. All nests with chicks that could be aged with confidence were included in the analysis, irrespective of the data source. The age of nestlings can be estimated by size, colour, and feather development, which are techniques utilised for many raptor species, including the wedge-tailed eagle (Sergio & Bogliani 1999; Olsen 2005; Penteriani et al. 2005; Debus et al. 2007; Bionda & Brambilla 2012). Hatching dates were obtained by backdating from feather development of nestlings (Steenhof & Newton 2007), while the start date of incubation was obtained by subtracting 45 days, the average incubation period, from the hatching date (Debus et al. 2007; Koch, Wiersma & Munks 2012). Given changes in the availability of data, the number of chicks included in the breeding timing for each year was variable (Table 1) (Koch, Wiersma & Munks 2012).
Breeding success

To assess the breeding success of the Tasmanian wedge-tailed eagle, nests were selected from the Raptor Nest Database in a variety of land use types, including state forest and private land across Tasmania (DPIPWE 2013). The nests were monitored from a fixed wing aircraft during November and early December each year from 2007-2013 by the Tasmanian Forest Practices Authority (FPA) (Koch, Wiersma & Munks 2012). The nests surveyed varied slightly between years (Table 1). Nests that could be adequately surveyed (i.e. a good view into the nest was achieved) were classified into one of two categories: nests containing a nestling were considered successful, while nests not containing a nestling were considered unsuccessful. Unsuccessful nests include both those where breeding was attempted and failed and nests that were not attempted at all. An additional classification was added during the 2012 breeding season, where nests that were unsuccessful were also defined as having “recent material” or “no recent material” to estimate nest usage in addition to nest success.

In an effort to include only independent nests, of those that were surveyed in the same year and were less than 3 km apart, only a single nest was included in the analysis (nests with more years of data were selected). Nests within 3 km of one another are likely to be within the same breeding territory as the estimated wedge-tailed eagle territory size is 30 km² in optimal habitat (Bell & Mooney 1999). However, some territories may be larger, so it is possible that some nests included in the analysis belonged to the same breeding territories. More details regarding methods of nest selection and survey used during the first 5 years of monitoring can be found in Koch, Wiersma and Munks (2012).
Figure 1. The location of wedge-tailed eagle nests (n=292) included in the current study. Nests were surveyed via aircraft between 1 and 7 times throughout the survey period (2007-2013).

Table 1. The number of wedge-tailed eagle nests included in the modelling of the breeding success and timing from each year of surveys.

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of nests included in breeding success analysis</th>
<th>Number of nests included in breeding timing analysis</th>
</tr>
</thead>
<tbody>
<tr>
<td>2007</td>
<td>86</td>
<td>31</td>
</tr>
<tr>
<td>2008</td>
<td>68</td>
<td>12</td>
</tr>
<tr>
<td>2009</td>
<td>139</td>
<td>26</td>
</tr>
<tr>
<td>2010</td>
<td>126</td>
<td>22</td>
</tr>
<tr>
<td>2011</td>
<td>145</td>
<td>20</td>
</tr>
<tr>
<td>2012</td>
<td>141</td>
<td>50</td>
</tr>
<tr>
<td>2013</td>
<td>139</td>
<td>36</td>
</tr>
</tbody>
</table>
Environmental variables

I developed a preliminary set of 10 candidate environmental variables considered likely to influence the breeding success of the Tasmanian wedge-tailed eagle, based on findings for similar species as outlined in the Introduction. I included variables describing climate, disturbance, prey availability, and number of nearby nests. A subset of the predictor variables expected to influence nest success, specifically rainfall, temperature, and prey availability, is also likely to influence the timing of the breeding season (Steenhof, Kochert & McDonald 1997).

Climatic variables were obtained for each of the nest coordinates from the Australian Water Availability Project database (Raupach et al. 2009). The variables considered were monthly minimum recorded temperatures (°C), and total monthly rainfall (mm) for winter (June-August) and spring (September-November) of each year, since these variables and seasons have been shown to impact the breeding success of other raptors (Steenhof, Kochert & McDonald 1997; Bionda & Brambilla 2012).

The level of human disturbance at each nest site was estimated by calculating two measures of roads near each nest, as the presence of roads is generally correlated with increased use of areas by humans (Trombulak & Frissell 2000). Road presence was determined using the LIST 2009 Transport Layer as maintained by the Department of Infrastructure, Energy, and Resources using ArcGIS v 10.1 (ESRI 2013). All road classes and types were considered, from highways to unsealed private roads, but walking tracks were excluded. The first measure used the total length of roads (m) within 1 km of each nest, while the second is the distance (m) between each nest and the nearest road.

Prey availability was estimated from the Department of Primary Industries, Parks, Water and Environment’s spotlighting data. From 1985 to the present, native and non-native mammal observations across Tasmania were recorded through spotlighting once-yearly from a vehicle along 10 km line transects during November-March (Southwell & Fletcher 1993). I obtained a mean of the prey counts at each transect for the total number of yearly surveys conducted, including all native and non-native species. For each year of interest, the relative prey abundance was calculated by taking a ratio of the given year’s total prey count and dividing it by the overall mean for that transect to give
an estimate of the yearly variation from the mean. In order to reduce the random variation that can occur from transect to transect, the prey abundance for each nest was estimated as a mean of the nearest 6 transects to each nest.

The final predictor I examined was the number of known nests within 3 km of each nest, as an estimate of the number of alternative nests in each breeding territory. This information was collected using data from the raptor nest database (DPIPWE 2013).

Each of the continuous variables was examined for normality. In an effort to improve the normality of the variables with non-normal distributions, data were either log-transformed or square root transformed. No highly correlated variables (Pearson’s correlation coefficient, r > 0.7) were included in the models to avoid instability in parameter estimation (Quinn & Keough 2002). To determine which of the correlated variables to include in the analysis, I used R (R Core Team 2013) and the lme4 package (Bates et al. 2014) to compare generalized linear mixed effects models (GLMMs) of single variables. Models containing each correlated variable were compared, and those with lower AIC values were used for later models. As a result of this preliminary correlation analysis, four predictor variables were removed from candidacy, leaving six variables as candidates for further modelling of breeding success, and three for modelling breeding timing (Table 2).
Table 2. Environmental variables included in wedge-tailed eagle breeding success and breeding timing modelling, with transformations done and expected impacts. All variables listed were included in modelling breeding success; those marked with * were also used to model breeding timing.

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Predictor variable description</th>
<th>Transformation</th>
<th>Expected response on success</th>
<th>Expected response on timing</th>
</tr>
</thead>
<tbody>
<tr>
<td>roads 1k</td>
<td>Total distance of roads (m) within 1 km of nest</td>
<td>Square root</td>
<td>Positive</td>
<td></td>
</tr>
<tr>
<td>near nests</td>
<td>Number of nests within 3 km of nest</td>
<td>None</td>
<td>Negative</td>
<td></td>
</tr>
<tr>
<td>winter rain</td>
<td>Total amount of winter rainfall (mm)</td>
<td>Square root</td>
<td>Negative</td>
<td></td>
</tr>
<tr>
<td>spring rain*</td>
<td>Total amount of spring rainfall (mm)</td>
<td>Square root</td>
<td>Negative</td>
<td>Delayed</td>
</tr>
<tr>
<td>winter min.*</td>
<td>Winter mean minimum temperature (ºC)</td>
<td>None</td>
<td>Positive</td>
<td>Delayed</td>
</tr>
<tr>
<td>prey*</td>
<td>Relative prey availability</td>
<td>Square root</td>
<td>Positive</td>
<td>Earlier</td>
</tr>
</tbody>
</table>

*Behavioural observations*

Methods to observe eagle behaviour on the nest involved practices not normally permitted for standard eagle nest activity surveys. All efforts were made to design methods that would minimise additional disturbance, as detailed below, but it was recognised that the work might present a risk to eagle breeding success. Methods were reviewed and approved by both the Threatened Species and Marine Section and Animal Ethics Committee of DPIPWE on the basis of the anticipated conservation benefits of the findings, and the recognition that this research would involve a one-off procedure rather than a standard, widely used approach.

Over 40 potential nest sites from the Raptor Nest Database were identified for this study (DPIPWE 2013). Aerial survey data and forest planner knowledge were used to select potential nest sites based on the presence of good viewing points into the nest, and nests
that have been regularly used by breeding birds in the past. Each of the potential nests was visited in August or the first week of September to assess if it was likely to be used in the 2013 breeding season. If a good vantage point was found and there was evidence that the nest might be used for breeding (e.g. had recent nesting material added, Gaffney & Mooney 1992), a small tent was erected 100-200 m from the nest. Efforts were made to ensure the nest assessment and tent erection created minimal disturbance. If eagles were present at or around nest sites, a tent was only erected if it could be done in less than 20 minutes in order to reduce the amount of time spent in the vicinity of the nest site. This provision was only required at a single nest, at which eagles had already commenced incubation.

Behavioural observations from the hides were done during the incubation and early nestling stages of the breeding season, when adults were consistently attending nests. The activity status of each nest (i.e. whether or not the nest is in use during a particular breeding season) was also recorded for each of the study sites. During the behavioural observations nests were recorded as active if there was an incubating bird at the nest and the presence of eggs or chicks was determined. If there were no eagles present and no signs of recent use on the nest, nests were recorded as inactive. The distance between each study nest and the nearest road was recorded as an estimate of the level of human disturbance for each site. Of the 16 nests selected for the study, 12 were active and 4 were not active during the 2013-2014 breeding season (Figure 2).
Figure 2. Tasmanian wedge-tailed eagle nests included in the behavioural study and their activity status (black = active, n=12; red = inactive, n=4) during the 2013-2014 breeding season.

The nearest vehicle access point was a minimum of 300 m from each nest and out of line-of-sight. For the behavioural surveys I walked to the hide accompanied by a co-researcher. Once we arrived at the hide, I entered and began to record behavioural data, while the co-researcher returned to the vehicle. Having an accompanying person to leave the hide after I had entered it was recommended by wedge-tailed eagle experts as a technique established to minimise disturbance to sensitive bird species. The goal of this ‘walk-in’ technique is for the birds to view the second person leaving the vicinity of the nest and subsequently return to an ‘undisturbed’ state (Beer 1961).

The study began when the incubation phase was expected to be underway, and finished when the chicks produced were approximately 4 weeks old (the start of October until the first week of December). Nests were not visited during the period likely to be the first week of incubation to minimise the level of disturbance at this more sensitive time period (Richardson & Miller 1997).

I employed a combination of sampling methods to record behavioural observations. Each survey period lasted approximately 2.5 hours. To get an estimate of the time eagles engaged in prolonged behaviours, or states, the “scan sampling” method was
employed. For this method the eagle’s activities were recorded at 5 minute intervals in order to determine the percentage of time spent in certain activities. Examples of behavioural states include sitting on the nest, or preening. Because the scan sampling method tends to underrepresent shorter-lasting behaviours, or behavioural events, I also employed the “all-occurrence” method to record each time that behavioural events occurred, along with a corresponding time. From the all-occurrence method, I obtained a frequency of the behavioural events. Examples of behavioural events include vocalisations, or arrivals and departures from the nest. The combination of the two methods enabled me to record not only a frequency of behaviours that occurred, but also the time spent engaged in each behaviour. In the event of a flushing response, the time to return (defined as the length of time an adult was away from the nest after flushing) was calculated. Behaviours were divided into two categories: relaxed and disturbed, based on a priori recommendations from wedge-tailed eagle experts and reviewing literature that documented common raptor responses to disturbance (Table 3).
Table 3. Terminology used in describing breeding behaviours of Tasmanian wedge-tailed eagles, along with their categorisation into ‘relaxed’ or ‘disturbed’ categories, if applicable.

<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
<th>Relaxed/Disturbed (source)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sitting on the nest</td>
<td>Sitting in nest bowl, either incubating or brooding</td>
<td>n/a</td>
</tr>
<tr>
<td>Standing on the nest</td>
<td>Adults attending to nest, but standing off to side</td>
<td>n/a</td>
</tr>
<tr>
<td>Flushing</td>
<td>Flying off the nest, leaving nest unattended</td>
<td>Disturbed (Steidl &amp; Anthony 2000; Whitfield, Ruddock &amp; Bullman 2008; Grubb <em>et al.</em> 2010)</td>
</tr>
<tr>
<td>Nest maintenance</td>
<td>Arranging nest material, or removing old prey items from nest</td>
<td>Relaxed (Steidl <em>et al.</em> 1993; Steidl &amp; Anthony 2000)</td>
</tr>
<tr>
<td>Rousing</td>
<td>Fluffing out and shaking feathers (common when wet)</td>
<td>Relaxed (B. Brown, and J. Wiersma, pers. comm)</td>
</tr>
<tr>
<td>Shuffling</td>
<td>Readjusting body positioning while seated on nest; can be turning eggs but not usually visible</td>
<td>Relaxed (B. Brown, and J. Wiersma, pers. comm)</td>
</tr>
<tr>
<td>Preening</td>
<td>Self-grooming; dressing feathers with the beak</td>
<td>Relaxed (Steidl <em>et al.</em> 1993; Steidl &amp; Anthony 2000)</td>
</tr>
<tr>
<td>Feeding</td>
<td>Consuming prey or feeding chicks on the nest</td>
<td>Relaxed (Steidl <em>et al.</em> 1993; Steidl &amp; Anthony 2000)</td>
</tr>
<tr>
<td>Ducking down</td>
<td>Flattening down into the nest</td>
<td>Disturbed (Ellis 1981; Grubb <em>et al.</em> 2010)</td>
</tr>
<tr>
<td>Head bobbing</td>
<td>Rapidly raising and lowering head</td>
<td>Disturbed (Manning &amp; Kaler 2011)</td>
</tr>
<tr>
<td>Sitting upright</td>
<td>Sudden change in body position to an alert upright stance</td>
<td>Disturbed (Ellis 1981; González <em>et al.</em> 2006a; Whitfield, Ruddock &amp; Bullman 2008)</td>
</tr>
<tr>
<td>Vocalisation</td>
<td>Calling; typically during territory defence or communication within a breeding pair</td>
<td>Disturbed (Ellis 1981; Gaffney &amp; Mooney 1992; Grubb &amp; Bowerman 1997; Steidl &amp; Anthony 2000)</td>
</tr>
<tr>
<td>Nest changeover</td>
<td>When one eagle returns to the nest and switches with attending eagle, which then departs</td>
<td>Relaxed (Grubb <em>et al.</em> 2010)</td>
</tr>
</tbody>
</table>
Due the chance that eagles would flush from the nest due to our approach, nests were only visited on days with favourable weather conditions, i.e. non-rainy days with temperatures between 8°C and 32°C, as inclement weather can increase the risk of nest failure (Pagel, Whittington & Allen 2010). Precautions also included a commitment to leave the study nests if our approach caused the eagles to flush from the nest for a prolonged period of time, leaving eggs or chicks exposed. On warm (>20°C) non-windy days, birds could be absent from the nest for up to 50 minutes before I had to leave the observation point. If birds flushed for longer than the 50 minute time period at multiple nests (>3), then we would change our approach and access the hides before dawn to further minimise disturbance to the birds.

Breeding results were also recorded by aerial survey as described above. Active nests that successfully raised a chick until the end of the observation period (end of November) were recorded as successful. Active nests with either eggs that did not hatch or chicks that did not survive until the end of the observation period were recorded as breeding failures.

**Data analysis**

**Breeding timing and success**

To model the timing and success of the breeding season, I used mixed effects modelling techniques, using the *lme4* package (Bates et al. 2014) in the program R (R Core Team 2013). For the timing model, I used linear mixed effects modelling (LMM) with a Gaussian response variable (the start date of incubation). For the breeding success model, I used generalised linear mixed effects modelling (GLMM) with a binomial response variable (successful=1, unsuccessful=0). The fixed effects were the environmental variables outlined in (Table 2) and NestID and Year were the random effects.

For each set of analyses I first fit a global model, which included all relevant environmental variables as fixed effects (Table 2). I then used the R package *MuMIn* (Barton 2013) to generate a complete set of candidate models, which included all possible combinations of the fixed effects from the global model without changing the random effects. Though the “all subsets” approach has been warned against (Burnham...
it is appropriate in this case, because all environmental variables were selected with \textit{a priori} reason to expect that they are influential to the timing and success of the breeding season.

The set of best-fitting candidate models were selected based on the Akaike information criterion (AIC) values, where smaller AIC values indicate better, more parsimonious models (Quinn & Keough 2002). The ratio of observations to the number of covariates (breeding timing: 197/3; breeding success: 844/6) were sufficiently large for the AIC to be an appropriate selection criterion compared to alternatives (e.g. AICc) (Burnham & Anderson 2002). In this case, LMM and GLMM resulted in a large number of closely related models, and designation of a single best model via traditional model selection techniques, including stepwise regression, was unsatisfactory because this technique ignores the uncertainty that arises when two or more models have similar support (Johnson & Omland 2004; Bolker \textit{et al.} 2009). According to Burnham and Anderson (2002), selecting a single best model is not ideal unless the best model has an Akaike weight ($w_i$) greater than 0.9. In order to account for the uncertainty in identification of an ‘optimal’ model, I took a model averaging approach using the \textit{MuMIn} package (Barton 2013). Coefficients and standard errors were averaged over the entire set of candidate models, producing more robust parameter estimations and predictions of the timing of the breeding season than simply choosing the model with the lowest AIC (Johnson & Omland 2004; Anderson 2008).

In addition to determining the best model, or set of models using model averaging, I also examined the relative variable importance using the \textit{MuMIn} package in R (Barton 2013). Akaike weights ($w_i$) were determined for each candidate model, which represent the likelihood that a given model is the best model for the observed data out of the set of candidate models (Burnham & Anderson 2002). I obtained the relative variable importance by summing $w_i$ for all of the candidate models in which the variable of interest appeared.

I evaluated LMMs qualitatively by visual inspection of residual plots for deviations from homoscedasticity or normality, an approach ineffective for GLMMs due to a binomial response variable. To evaluate model fit, conditional pseudo-$R^2$ values of top-ranked GLMMs and LMMs were calculated using the \textit{MuMIn} package in R (Barton 2013).
**Behavioural study**

Given the small amount of data collected, quantitative analyses were not appropriate, so results are presented qualitatively. Observations from each nest were pooled to give an overall description of the breeding behaviour of the eagle at that nest, with distinctions made for whether the observations occurred during the incubation period or early nestling period of the breeding season. The frequency per hour for each behavioural event is calculated for each breeding period (note: this does not indicate the amount of time spent, only the number of times this behaviour was initiated). The activity budget, which gives a percentage of time spent engaged in each behavioural state, is also presented for each breeding period.

Time spent engaged in relaxed vs. disturbed behaviours were totalled for each nest for each visit. Frequencies of relaxed vs. disturbed behaviours were also totalled for each visit. The time to return from flushing from each nest was compared between visits to investigate whether the behavioural response to the approach increased or decreased with repeated disturbance. Potential relationships between 1) the behavioural responses to disturbance at each nest and the result of the breeding attempt for each active nest; and 2) the distance to the nearest road versus the result of the breeding attempt for each active nest were visually examined for any trends.
3. Results

Breeding timing

The full set of eight competing models included all combinations of the three environmental variables (winter min., prey, and spring rain) (Table 4). The strongest model, $M_8$, included all three environmental variables. $M_8$ has an Akaike weight ($w_8$) of 0.656, which is considerably higher than the next best model $M_6$ ($w_6 = 0.182$). The $\Delta AIC$ between $M_8$ and $M_6$ is 2.51, indicating that $M_6$ and all subsequent models have considerably less empirical support from the data than the best model (Burnham & Anderson 2002). Visual inspection of residual plots for the best model did not result in any obvious deviations from normality or homoscedasticity, indicating that the model did not violate any assumptions of the LMM. The conditional pseudo-$R^2$ value calculated for $M_8$ was 0.229, indicating that prey, spring rain, and winter minimum, along with the random effects, explained over 22% of the variation in the timing of the breeding season.

Table 4. The global model set for predicting the timing of the breeding season of the Tasmanian wedge-tailed eagle. Coefficient estimates, AIC values, and Akaike weights are given. Random effects, Nest ID and Year, are included in all models. Square root transformations were performed on prey and spring rain.

<table>
<thead>
<tr>
<th>Model</th>
<th>Intercept</th>
<th>prey</th>
<th>spring rain</th>
<th>winter min.</th>
<th>df</th>
<th>logLik</th>
<th>$\Delta AIC$</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>8</td>
<td>65.57</td>
<td>3.70</td>
<td>0.80</td>
<td>-1.20</td>
<td>7</td>
<td>-745.0</td>
<td>0</td>
<td>0.656</td>
</tr>
<tr>
<td>6</td>
<td>76.93</td>
<td>4.34</td>
<td></td>
<td>-1.07</td>
<td>6</td>
<td>-747.3</td>
<td>2.56</td>
<td>0.182</td>
</tr>
<tr>
<td>7</td>
<td>67.96</td>
<td>0.86</td>
<td></td>
<td>-1.13</td>
<td>6</td>
<td>-748.1</td>
<td>4.17</td>
<td>0.081</td>
</tr>
<tr>
<td>4</td>
<td>65.60</td>
<td>3.18</td>
<td>0.64</td>
<td></td>
<td>6</td>
<td>-748.1</td>
<td>5.88</td>
<td>0.035</td>
</tr>
<tr>
<td>2</td>
<td>74.96</td>
<td>3.72</td>
<td></td>
<td></td>
<td>5</td>
<td>-750.4</td>
<td>6.81</td>
<td>0.022</td>
</tr>
<tr>
<td>5</td>
<td>80.67</td>
<td></td>
<td>-0.965</td>
<td></td>
<td>5</td>
<td>-750.8</td>
<td>7.65</td>
<td>0.014</td>
</tr>
<tr>
<td>3</td>
<td>67.74</td>
<td>0.69</td>
<td></td>
<td></td>
<td>5</td>
<td>-751.6</td>
<td>9.26</td>
<td>0.006</td>
</tr>
<tr>
<td>1</td>
<td>78.38</td>
<td></td>
<td></td>
<td></td>
<td>4</td>
<td>-753.5</td>
<td>10.87</td>
<td>0.003</td>
</tr>
</tbody>
</table>

Each of the three predictor variables had a variable importance weight >0.75 (Figure 3b). Prey abundance and average winter minimum temperature carried higher variable importance weights than spring rain due to their inclusion in both the top two models, which together carried over 80% of the Akaike weight.
Since there was still some uncertainty in selecting the best model from the candidate models, \( w_k < 0.9 \) (Burnham & Anderson 2002), I averaged the breeding timing LMMs to gain a more robust estimate of the effects of each predictor variable (Table 5, Figure 3). As predicted, the start date of incubation was delayed by higher total spring rainfall (Figure 4a) and was earlier with warmer winters (Figure 4b). Contrary to expectations, higher relative prey availability was linked to a later start date of incubation. However, this relationship was highly variable between models, resulting in a high standard error, and the 95% confidence interval overlapped with zero, which indicates a non-significant relationship (Figure 3a).

Table 5. Model averaged coefficient estimates and standard errors of the environmental variables used in the linear mixed model of Tasmanian wedge-tailed eagle breeding timing. In bold type are the estimates significantly different from zero \( (p < 0.05) \).

|               | Estimate | Std. Error | z value | Pr(>|z|) |
|---------------|----------|------------|---------|----------|
| (Intercept)   | 68.260   | 6.847      | 9.969   | < 2e-16  |
| spring rain   | 0.798    | 0.328      | 2.429   | 0.015    |
| winter min.   | -1.153   | 0.427      | 2.698   | 0.007    |
| prey          | 3.998    | 2.220      | 1.818   | 0.069    |

![Figure 3. (a) Regression coefficients for each predictor variable for breeding timing, averaged across all competing model combinations, weighted by their AIC score, together with 95% confidence intervals. (b) Relative variable importance across all eight models predicting timing of the breeding season. Values of 1.0 indicate greatest relative importance.](image)
Figure 4. The predicted start date of incubation for the Tasmanian wedge-tailed eagle in relation to (a) spring rainfall and (b) mean winter minimum temperature. Raw data are indicated by circles, and the red line is the linear model, with averaged intercept and coefficients for each variable. Only statistically significant variables are illustrated.

Breeding success

Of the full set of 64 competing models, the top-ranking seven models had ΔAIC<2 (Table 6). The top ranked model (M22) included three variables: near nests, spring rain, and winter min., all of which were inversely related to breeding success. The conditional pseudo-$R^2$ value calculated from the top model was 0.325, which indicates that M22 explained over 32% of the variation in the data. However, M22 had an Akaike weight of just 0.115. This low model weight, coupled with the high number of models within two AIC values of the top model indicated considerable model uncertainty. Subsequently, a model averaging approach was used, which averaged intercepts and coefficients across the entire candidate set of models. For a list of all 64 candidate models see Appendix 1.
Table 6. The top ranked (ΔAIC<2) models predicting the nest success of the Tasmanian wedge-tailed eagle, along with coefficients, AIC values, and Akaike weights. Random effects, ‘Nest ID’ and ‘Year’, are included in all models. Square root transformations were performed on roads 1k, winter rain, spring rain, and prey.

<table>
<thead>
<tr>
<th>Model</th>
<th>Intercept</th>
<th>near nests</th>
<th>prey</th>
<th>spring rain</th>
<th>roads 1k</th>
<th>winter min.</th>
<th>winter rain</th>
<th>df</th>
<th>ΔAIC</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>22</td>
<td>0.591</td>
<td>-0.221</td>
<td>-0.115</td>
<td>-0.096</td>
<td></td>
<td></td>
<td></td>
<td>6</td>
<td>0</td>
<td>0.115</td>
</tr>
<tr>
<td>6</td>
<td>0.282</td>
<td>-0.207</td>
<td>-0.113</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>5</td>
<td>0.23</td>
<td>0.102</td>
</tr>
<tr>
<td>8</td>
<td>0.900</td>
<td>-0.201</td>
<td>-0.695</td>
<td>-0.111</td>
<td></td>
<td></td>
<td></td>
<td>6</td>
<td>0.78</td>
<td>0.078</td>
</tr>
<tr>
<td>24</td>
<td>1.090</td>
<td>-0.215</td>
<td>-0.604</td>
<td>-0.112</td>
<td>-0.088</td>
<td></td>
<td></td>
<td>7</td>
<td>0.91</td>
<td>0.073</td>
</tr>
<tr>
<td>54</td>
<td>0.513</td>
<td>-0.229</td>
<td>-0.141</td>
<td>-0.107</td>
<td>0.0293</td>
<td></td>
<td></td>
<td>7</td>
<td>1.49</td>
<td>0.054</td>
</tr>
<tr>
<td>30</td>
<td>0.671</td>
<td>-0.215</td>
<td>-0.115</td>
<td>-0.0017</td>
<td>-0.098</td>
<td></td>
<td></td>
<td>7</td>
<td>1.85</td>
<td>0.045</td>
</tr>
<tr>
<td>56</td>
<td>1.107</td>
<td>-0.225</td>
<td>-0.745</td>
<td>-0.148</td>
<td>-0.103</td>
<td>0.0422</td>
<td></td>
<td>8</td>
<td>1.93</td>
<td>0.044</td>
</tr>
</tbody>
</table>
Figure 5. (a) Regression coefficients for each environmental variable, averaged across all competing model combinations predicting breeding success, weighted by their AIC score, together with 95% confidence intervals [mean coefficients ±(unconditional standard error × 1.96)]. (b) Relative variable importance across all 64 models predicting breeding success. Values of 1.0 indicate greatest relative importance of variables.
Of the six environmental variables included in the analysis, the only two that had a significant effect association with nest success when averaged across all 64 weighted models are near nests and spring rain (Table 7, Figure 5a). Mean values for all other variables (winter minimum temperature, relative prey availability, total winter rainfall, and the total distance of roads within 1km of each nest) had confidence intervals that overlapped with 0, and thus there was no significant association with breeding success (Table 7, Figure 5a).

**Table 7.** Model averaged coefficient estimates, and standard errors, of environmental variables for the generalised linear mixed model of Tasmanian wedge-tailed eagle breeding success. Estimates significantly different from zero ($p < 0.05$) are in bold type.

|                        | Estimate | Std. Error | z value | Pr(>|z|) |
|------------------------|----------|------------|---------|----------|
| (Intercept)            | 0.529    | 0.927      | 0.571   | 0.568    |
| near nests             | -0.213   | 0.093      | 2.283   | 0.022    |
| spring rain            | -0.121   | 0.048      | 2.553   | 0.011    |
| winter min.            | -0.094   | 0.064      | 1.473   | 0.141    |
| prey                   | -0.704   | 0.571      | 1.233   | 0.218    |
| winter rain            | 0.020    | 0.045      | 0.431   | 0.667    |
| roads 1k               | -0.002   | 0.005      | 0.404   | 0.686    |

The results of the variable importance analysis confirm the results from model averaging (Figure 5). To determine the relative importance of each environmental variable in predicting the breeding success of the Tasmanian wedge-tailed eagle, I tested each of the 6 variables included in the model building. Variables with the highest relative importance (Figure 5b) were the total amount of spring rainfall and the number of near nests (within 3 km), with variable importance weights of 0.92 and 0.82 respectively out of a possible maximum of 1. The average winter minimum temperature was the third most important variable with a weight of 0.51. The rest of the variables, including the relative prey abundance, total distance of roads within 1km of each nest, and total amount of winter rainfall, had lower variable importance weights (Figure 5b).

As predicted, the total amount of spring rainfall and number of known nests within 3 km were both inversely related to breeding success (Figure 6). Contrary to expectations, there was an inverse trend between average winter minimum temperature and breeding success, although this relationship was not significant (Table 7).
Figure 6. The predicted likelihood that a chick was successfully raised at a given nest in relation to the amount of (a) spring rainfall and (b) number of nearby nests (within a 3km radius). Raw data are represented by empty circles in (a) and bars in (b): proportions of unsuccessful (dark) and successful (light) nests, with totals for each category in parentheses. The red lines are the inverse-logit functions fit by model averaged intercepts and coefficients. Only statistically significant variables are illustrated.

**Behavioural observations**

In October and November, behavioural surveys were conducted at 12 active nests. Eagles were observed on the nest for a total of 19 hours during the incubation stage of the breeding season, and for seven hours during the early nestling stage.

The most frequent behavioural event during incubation was vocalising (5.91/hour), followed by ducking the head down (3.74/hr) and sitting upright (2.48/hr) (Figure 7). The most frequent behavioural event during the early nestling stage was also vocalising (0.86/hr), followed by feeding (0.73/hr) (Figure 7).

For behavioural states I recorded activity time budgets. As expected, sitting on the nest was the most common behaviour both during incubation and the early nestling stages,
taking up 90% of the time spent on the nest during incubation and 67% during the early nestling stage (Figure 8). Standing on the nest was the second most prevalent behaviour (6% of the activity budget) during incubation, while feeding was the second most common behaviour (15%) during the early nestling stage (Figure 8).

**Figure 7.** The frequency per hour of each behaviour event observed for both the incubation (black) and early nestling periods (grey) of the Tasmanian wedge-tailed eagle. For behaviour definitions, refer to Table 3.

**Figure 8.** Proportion of time spent in various behavioural states on the nest by Tasmanian wedge-tailed eagles during the (a) incubation and (b) nestling stages of the breeding season. For behaviour definitions, refer to Table 3.
During behavioural surveys, flushing or leaving the nest was a common behavioural response to the observers approaching the hides, occurring at 9 of 11 nests that were active during the first visit (Figure 9). The 12th active nest was not included because although an incubating eagle was observed during the hide setup, breeding had failed by the time of the first behavioural survey visit (Nest 12, Figure 9). The duration of time that each eagle was away from the nest after flushing was highly variable between nests as well as between visits for single nests (Figure 9). For example, during the first visit to each nest two eagles did not flush in response to the approach, while one eagle flushed and did not return before the 50 minute threshold (the actual amount of time it was off the nest is unknown, but was at least 54 minutes).

In response to observers approaching the hides at three nests for the second visit, all eagles left the nest for longer than the 50 minute threshold, irrespective of the time to return during the initial visits. Due to the consistent pattern of extended periods off the nest occurring (presumably) as a result of the survey techniques, we had to abandon the survey method. As the survey methods had to be changed due to the impact on the birds, only these three nests were visited twice before we changed techniques and approached the hides before dawn to minimise disturbance.

Figure 9. The time to return after flushing from the nest by Tasmanian wedge-tailed eagles for each survey visit. Nests marked with * are nests where the eagles did not flush during the approach, while † indicates that a nest failed prior to the first behavioural visit. The dashed line at 50 minutes corresponds to the threshold at which I had to leave the nests, so each bar that crossed this threshold represents the time observed off the nest, and the total time to return is unknown.
In terms of breeding success, most study nests failed (n=10). The next most common outcome was no breeding attempt (n=4), with nest success being the least common outcome (n=2). Thus, of the nests where a breeding attempt was made, 83% failed and 17% were successful (Figure 11).

The limited behavioural data obtained (one visit at most nests) meant the behavioural analyses had to be qualitative. The prevalence of ‘relaxed’ vs. ‘disturbed’ behaviours were recorded as frequencies for behavioural events and as a percentage of time for the behavioural states, and varied considerably between nests (Figure 10). There was also variation in the proportion of time eagles spent off the nest at different nest sites (Figure 10). Of the two successful nests, one flushed without returning during the first nest visit (Nest 7, Figure 9), and so is excluded from this analysis due to a lack of behavioural data. However, there was no evidence of a link between nest success and a lower prevalence of ‘disturbed’ behaviours (Figure 9). In fact, the eagle observed at one successful nest exhibited the lowest frequency of relaxed behaviours and close to the lowest percentage of time spent engaged in relaxed behaviours of all the study nests during the first visit (Figure 10). This eagle also exhibited higher than average levels of disturbed behaviours, in both frequency and percentage of time. The eagles at this successful nest did however spend the lowest amount of time off the nest during the survey period, at just 4% of the 2.5 hours. However, the eagles at the only other successful nest spent the highest amount of time off the nest (100% of the survey time). This high variability between individuals limited the inferences that could be made from comparing behavioural responses and breeding outcomes.
Figure 10. (a) Frequencies and (b) percentage of time eagles spent engaged in relaxed behaviours, disturbed behaviours, and time spent off nest as observed during the first visit to each active wedge-tailed eagle nest. Nests are distinguished by their breeding result: black circles represent breeding failures, while red triangles represent the successful nest where behavioural data was collected.
Figure 11. The proportion of estimated breeding failures among Tasmanian wedge-tailed eagle nests aerially surveyed during the past two years, and nests included in behavioural surveys in 2013. Black columns represent the percentage of wedge-tailed eagle nests where breeding appeared to have been attempted and failed, based on evidence of recent nest use without the presence of a chick. The grey column is a definitive percentage of behavioural survey nests that attempted incubation and failed.

State-wide nest breeding failure rates for the two breeding seasons with data on evidence of recent nest material, were 55% in 2012 and 50% in 2013. A significantly higher proportion of attempted breeding failures was observed within the behavioural study than within the aerial study from the 2013 breeding season ($\chi^2 = 4.644, p = 0.031$) with 83% of the 12 active behavioural study nests resulting nest failure (Figure 11).

It is possible that an even stronger difference in the rate of nest failure existed between the two survey methods in 2013 than is suggested in Figure 9. The successful nests from the aerial surveys include all nests where chicks were observed. Since the aerial surveys only occurred at the end of the breeding season, the nests classified as attempted and failed were nests recorded with evidence of recent use with no chicks present. It is likely that this estimate includes some nests that were maintained by the breeding pairs but in which no breeding attempt was made. However, correcting this potential bias would result in a lower number of “attempted failed” nests, which would result in a more pronounced difference between the study nests and the aerials survey nests.
To identify any differences between the nests included in the behavioural study that could explain the breeding results, I examined the distance to the nearest road from each nest as a possible explanatory variable and proxy for long-term disturbance levels (Figure 12). One of the two successful nests was much further from roads than all other sites. However, with the limited sample size (n=16), the inferences that can be made from the results are very weak.
4. Discussion
To breed successfully, eagles require suitable biotic and abiotic conditions that allow them to remain on the nest for a sufficient duration to incubate and rear offspring. I found that abiotic conditions, primarily spring rain and winter temperatures, affected breeding eagles as predicted. However, the primary biotic variable influencing breeding eagles was not prey availability, but instead was disturbance at the nest site. While wedge-tailed eagles were sensitive to disturbance, the small sample of birds studied could not link the behaviour of the birds on the nest to the likelihood of nest failure, perhaps because disturbance can be expressed in different ways. Interactions between biotic and abiotic variables may contribute to the variability of nest success seen over the years in Tasmania.

Breeding timing
The timing of the breeding season in bird species can influence subsequent breeding success. For the Tasmanian wedge-tailed eagle, breeding timing was related to spring rainfall and winter temperatures, but not prey availability. Successful breeding attempts tended to be later in the season if spring rainfall was high, which could be due to a later onset of incubation, or high failure rate of early breeding attempts. Tasmanian wedge-tailed eagles may start incubation later when spring rainfall is elevated, with a similar association in non-raptor bird species (Ost et al. 2008), but not in the closely related golden eagle (Steenhof, Kochert & McDonald 1997). Typically, rainfall is strongly linked to the onset of incubation in arid environments, where birds respond positively to rainfall and may even require rainfall before incubation can commence (Zann et al. 1995), which would not apply to the Tasmanian wedge-tailed eagle. Since breeding timing data in the current study were determined from surveys of chicks at the end of each breeding season, the observed delay in the timing of the breeding season could be biased. High intensity rainfall during early spring could disadvantage earlier breeders by promoting opportunities for nest failure due to egg and chick exposure over the incubation and early nestling stages (Radford & Plessis 2003). Thus, the observed age of chicks on successful nests, and the subsequent extrapolation of the average start date of incubation could be ‘delayed’ because the earlier incubating breeding pairs were unsuccessful and not detected in the data. Additionally, as raptors can successfully re-attempt to breed within a single season if the initial failure is early enough (Martinez &
Blanco 2002; Steenhof & Peterson 2009), nest failures caused by heavy rainfall early in the season could be re-attempted, and if successful, delay the observed timing of the breeding season. With the data available, it is not possible to distinguish between a real or perceived delay in breeding with high spring rain. However, as high rainfall is also correlated with lower nest success, the second explanation seems more likely to account for the observed delay.

Colder winter temperatures corresponded to delayed breeding, which could be due to later incubation start dates or prolonged incubation from slower embryonic development. Delayed incubation start dates after cold winters have been found for the closely related golden eagle (Steenhof, Kochert & McDonald 1997), as well as a number of other raptor species (Kostrzewa & Kostrzewa 1990; Marti 1994; Fairhurst & Bechard 2005; Steenhof & Peterson 2009). It is possible that the egg laying date in the Tasmanian wedge-tailed eagle is based at least partially on temperature cues, which have been experimentally linked to incubation onset in many bird species (Visser, Holleman & Caro 2009). A second potential reason for the observed delay in the timing of the breeding season with colder winter temperatures, which were highly correlated with colder spring temperatures, is that colder incubation temperatures can extend the incubation period by slowing embryonic development (Deeming & Ferguson 1991; Martin et al. 2007). The plasticity of incubation periods can be dramatic. In a classic example of this plasticity, an incubation period normally lasting 50 days was reduced by 22 days as a result of higher nest attentiveness, and associated warmer incubation temperatures (Ward 1940). Thus, the incubation period can vary markedly for species with relatively long incubation requirements, like the Tasmanian wedge-tailed eagle. Since temperature is a common cue for birds to begin incubation, it is likely that colder winters correspond to later start dates. However, the perceived delay may also be influenced by longer incubation periods during cold springs, and further information on the plasticity of the incubation period for eagles is required.

Contrary to predictions, relative prey availability did not significantly explain any variation in the timing of the breeding season, in contrast to studies on other eagle species (Hansen 1987; Steenhof, Kochert & McDonald 1997). One possible explanation is that prey abundance is often more influential for specialist predators which rely on a single prey species (e.g. rabbits or voles) (Korpimäki & Norrdahl 1991; Ontiveros &
Pleguezneles 2000; González et al. 2006b). In contrast, Tasmanian wedge-tailed eagles are generalist and opportunistic predators (Gaffney & Mooney 1992). Therefore wedge-tailed eagles may be less vulnerable to changes in the abundance of particular prey species as they can supplement their diet with other species. However, it is also possible that the spotlighting surveys did not detect variation in prey abundances relevant to Tasmanian wedge-tailed eagles. Although the spotlighting surveys are the best available estimate of prey abundance on a state-wide level, they were designed specifically to monitor abundances of two native macropod species (Bennett’s wallaby, *Macropus rufogriseus*; Tasmanian pademelon, *Thylogale billardierii*) and one arboreal marsupial (brushtail possum, *Trichosurus vulpecula*) (Southwell & Fletcher 1993). Thus, counts from the spotlighting data may provide less accurate abundance estimates for rabbits, hares and cats, which comprise a large portion of Tasmanian wedge-tailed eagle prey (Gaffney & Mooney 1992). The surveys are also only conducted once a year at each transect during the summer months (November-April), a time which is not as likely to be as important to Tasmanian wedge-tailed eagle reproduction as winter and spring (Tjernberg 1983; Korpimäki & Norrdahl 1991). Therefore finer scale prey surveys are required to confirm whether prey availability is related to the timing of the breeding season for wedge-tailed eagles.

**Breeding success**

The estimated rate of breeding failure of attempted wedge-tailed eagle nests falls into the range of those observed for other eagle species. The breeding failure estimates from 2012 and 2013 were 55% and 50%, respectively. Breeding failure rates in other eagle species vary significantly between years and species: the golden eagle ranges from 20% to 68% (Kochert et al. 1999); and the bald eagle ranges from 52% to 93% (Hansen 1987; Steidl, Kozie & Anthony 1997). As survey methods and definitions of nest success and failure are not consistent between studies, direct comparisons are not possible. However, the studies done provide broader context to demonstrate common levels of nest failure in closely related species. The estimate of state-wide breeding failure in Tasmania was determined by calculating the ratio of nests that contained recent nesting material without chicks, versus nests with chicks present, as seen during aerial surveys conducted in November and early December. My estimate of state-wide breeding failure is not definitive, as recent material may not actually represent a breeding attempt,
meaning the percentage of nest failure obtained is likely to be lower in reality. The inclusion of false positives in the ‘nest failure’ category would result in overinflation of the breeding failure estimate, so true nest failure (whereby a breeding attempt is made but fails) is likely to be lower than reported here. However, it is possible that the observed rate of nest failure could be an underestimation, as aerial surveys are conducted when chicks are still nest dependent (Koch, Wiersma & Munks 2012) and some chicks may not fledge successfully. Therefore, further research is required, but it appears Tasmanian wedge-tailed eagles have similar failure rates to other eagles.

Wedge-tailed eagle nests were more likely to be successful when spring rainfall was lower, a link found in a number of raptor species (Kostrzewa & Kostrzewa 1990; Krüger 2004; Bionda & Brambilla 2012), but which contradicts to studies on the mainland subspecies Aquila audax audax (Ridpath & Brooker 1985; Robertson 1987). Nest success for the Tasmanian wedge-tailed eagle was not related to the total amount of winter rain. The degree to which rainfall can influence breeding success is variable and depends on the species and habitat in question (Olsen & Olsen 1992). Wedge-tailed eagles in arid regions may require a minimum amount of rainfall before they will initiate breeding, while in more temperate areas there may be a maximum amount of rain that is beneficial. The lower breeding success associated with spring rainfall in the Tasmanian wedge-tailed eagle may result from less efficient hunting in heavy rainfall (Kostrzewa & Kostrzewa 1990; Olsen & Olsen 1992), and/or a greater chance of egg cooling or nestling death. However, it is likely that rainfall does not significantly reduce hunting efficiency because if higher rainfall corresponded strongly to lower hunting efficiency during the winter one would expect fewer breeding attempts, but no significant relationship between winter rain and nest success was found in the current study. Thus, though rain is essential for wedge-tailed eagles in arid habitats, elevated spring rainfall may be detrimental in Tasmania by lowering offspring survival.

Cold winter temperatures are less influential on the breeding success of the Tasmanian wedge-tailed eagle than other closely related raptors, potentially due to Tasmania’s temperate winters. It appeared that colder winters were linked to higher breeding success, but the relationship was not significant. Previous studies on the closely related golden eagle found that fewer breeding pairs laid eggs and fewer breeding attempts were successful after severe winters (Steenhof, Kochert & McDonald 1997; McIntyre &
Schmidt 2012). However, the studies on golden eagle breeding occurred in areas with much harsher winters than occur in Tasmania. For example, in an Alaskan population of golden eagles, the winter temperature variable was defined as number of days that the temperature did not exceed -17.8°C (McIntyre & Schmidt 2012), whereas the average winter minimum temperature at nest sites in Tasmania from the survey years was 2.7 °C (based on AWAP temperature data; Raupach et al. (2009). Thus there may be a critical minimum temperature at which nest success begins to decline, but since Tasmania has relatively mild winters, this variable has comparatively little impact on the breeding success of the Tasmanian wedge-tailed eagle.

Prey availability influences breeding success in a number of raptor species (Martin 1987; Byholm & Kekkonen 2008; McIntyre & Schmidt 2012), including *A. a. audax* on mainland Australia (Ridpath & Brooker 1985; Robertson 1987), although prey abundances tend to be less influential in species with high diet plasticity (Ontiveros & Pleguezuelos 2000). Relative prey availability, estimated using data from spotlighting transects from the summer prior to the breeding season, was not a predictor of breeding success in the Tasmanian wedge-tailed eagle. As discussed in relation to the timing of the breeding season, this lack of relationship may be due to inadequacies in the data used for the current study or due to the broad foraging requirements of wedge-tailed eagles (Gaffney & Mooney 1992).

Nest success decreased with greater numbers of known wedge-tailed eagle nests within a 3 km radius. This relationship is likely due to the fact that a higher number of alternative nests within a given territory (estimated 3 km radius; Bell & Mooney 1999) reduces the chances that each nest in the territory will be used in a given year. However, there is a long standing hypothesis that eagles will abandon nests where they are disturbed, which results in nest-switching or nest building (Brown 1976; Newton 1979; Mooney & Holdsworth 1991). Thus, the number of nests within a given territory may increase with the level of disturbance the eagles have been exposed to, as has been found for goshawks (Saga & Selås 2012), though support for this hypothesis in eagles is limited (Ontiveros, Caro & Pleguezuelos 2008b; Kochert & Steenhof 2012). The ten study nests that failed during the 2013 breeding season should be surveyed in the future to determine nest reuse after a definitive failure, and provide evidence to test the nest switching hypothesis.
Nest success was not related to the total length of roads within 1 km of each nest (highly correlated with the distance to nearest road) contrary to findings from other raptor species (González, Bustamante & Hiraldo 1992; Martinez, Pagan & Calvo 2006; Strasser & Heath 2013). However, there was no available data for road usage, only for existence of roads, and determining road usage would be a better proxy for estimating disturbance (González, Bustamante & Hiraldo 1992; Krüger 2004). Under current management prescriptions, use of forestry roads within 500 m or 1 km line-of-sight of the nest is restricted during the breeding season (FPA 2012), meaning the presence of roads may be a poor proxy for road use. The lack of evidence supporting a relationship between road density and breeding success for Tasmanian wedge-tailed eagles may suggest that this management prescription is effective. However, road restrictions do not apply to public roads, and are not enforced on agricultural roads. A clearer picture might be gained if the extent to which nests are affected by these restrictions during the breeding season could be gauged.

An alternative explanation for why road density did not have an impact on breeding success is that roads may be correlated with optimal habitat or prey availability, in the form of road-kill (Bautista et al. 2004). Tasmanian wedge-tailed eagles tend to have higher breeding success at nests with more agricultural land (and accompanying roads) nearby, likely due to more optimal foraging habitat within the territory (Koch, Wiersma & Munks 2012). This preference for open foraging habitat is common in large raptor species, including the golden eagle (Watson 1997; Whitfield et al. 2001). Wedge-tailed eagles are known to feed on carrion (Gaffney & Mooney 1992), so higher road density in a territory may increase food availability. The prevalence of carrion is plentiful in Tasmania, particularly with the decline of the Tasmanian devil, one of the state’s principal scavengers (Rounsevell, Taylor & Hocking 1991; Jones et al. 2007). Depending on the amount of carrion in the diet of the wedge-tailed eagle, the benefit of road-kill within a given territory could offset any detrimental effects of disturbance.

Finally, vehicular traffic may not be as disturbing to wedge-tailed eagles as pedestrian activities, such as hiking. This distinction is evident in the Spanish imperial eagle, *Aquila adalberti* (González et al. 2006a), the bald eagle (Grubb & King 1991; Steidl & Anthony 2000), and the common buzzard, *Buteo buteo* (Krüger 2004). The adverse behavioural response to humans may be because birds perceive humans as potential
predators and respond accordingly, even though this predation risk is not generally realised (Beale & Monaghan 2004). The association with humans as predators could be a lingering effect of human-related persecution. Although persecution is declining in many areas (Starker Leopold & Wolfe; Mooney & Holdsworth 1991; Foster & Wallis 2010), historic killing of tolerant individuals may have selected for lower tolerant birds (Kenney & Knight 1992; Foster & Wallis 2010). To summarise, breeding success was linked with rainfall and nest density, but much of the variability in the data remains unexplained. Thus, further study is required to investigate other potential factors and to confirm these findings, particularly regarding the impact of roads and prey.

**Breeding behaviour and response to disturbance**

Breeding behaviour should have been selected to increase breeding success and adult fitness. However, in long-lived raptors, adult survival is prioritised over offspring survival, as adults are likely to breed again (Blas, Sergio & Hiraldo 2009; Sergio et al. 2011). Thus the breeding behaviour of raptors is determined by compromising between trade-offs supporting offspring and adult fitness, which can change according external factors, notably human disturbance and stress (Breuner 2010).

Incubation requires higher nest attendance than hatched nestlings, particularly as chicks develop (Williams 1996). In the current study the time that eagles were observed sitting on the nest decreased between the incubation and the nestling stage, as expected. The observed decline in nest attendance corresponds to changes in time allocation in *Aquila audax audax* (Debus et al. 2007) and other raptor species (Levenson 1979). The behavioural observations from the incubation and early nestling periods in the current study indicated a high frequency of vocalisations, sitting upright, preening, and ducking head down. With the exception of preening, all of these behaviours are categorised as ‘disturbed’ behaviours. The behaviours categorised as ‘disturbed’ or ‘relaxed’ were based on recommendations from wedge-tailed eagle experts and on behaviours commonly related to experimental disturbances in related species (Ellis 1981; Steidl et al. 1993; Grubb & Bowerman 1997; Steidl & Anthony 2000; González et al. 2006a; Grubb et al. 2010; Manning & Kaler 2011). The prevalence of disturbed behaviours in the current study was confounded by the disturbance caused by the researchers approach to the hides prior to the behavioural monitoring. It is likely that the ‘disturbed’ behaviours predominant in our observations, particularly vocalisations, occur less
frequently during undisturbed incubation while ‘relaxed’ behaviours, such as nest maintenance and feeding would increase (Steidl & Anthony 2000).

There was no evidence of a link between the result of a breeding attempt and the prevalence of ‘disturbed’ or ‘relaxed’ behaviour on nests or behavioural responses to disturbance. However, I suggest that some of the behaviours may have been incorrectly categorised as either ‘relaxed’ or ‘disturbed,’ particularly if any were actually displacement activities. Displacement behaviours occur outside of their normal context, and instead occur uncharacteristically in situations of conflict (Martin 1987). They often consist of comfort behaviours (e.g. preening) in response to stress, instead of fleeing (Duncan & Wood-Gush 1972; Martin 1987). Displacement preening, i.e. preening during a stressful situation, tends to occur at a higher frequency and in shorter bursts, compared to typical preening (Duncan & Wood-Gush 1972). I hypothesise that under non-disturbed situations, wedge-tailed eagles will exhibit lower frequencies of preening bouts, but the overall preening episodes will account for a greater proportion of time than what was observed post-disturbance in this study. To eliminate observer bias, assessing this hypothesis would have to be done remotely (e.g. using video surveillance).

The technique used to approach the hides was designed to minimise disturbance, but still disturbed the Tasmanian wedge-tailed eagle. The ‘walk-in’ technique involved the surveyor approaching the hide another researcher who departed after the surveyor entered the hide. Although the ‘walk-in’ technique was adopted to minimise the impact on breeding birds (Beer 1961), it is possible that rather than minimising the impact of the observers approaching the hide, the technique resulted in higher disturbance. Because many eagles flushed off the nest, the presence of the accompanying person and vehicle within the eagles’ territory could have prevented some of the eagles from returning to the nest even though they were not in line-of-sight of the nest. Constructing the hides further away, which has been done successfully in other studies on sensitive raptors (González et al. 2006a; Bird 2007), was not possible at the study nests due to either obstructed views by vegetation or topographical limitations. We attempted to approach the hides prior to sunrise after it was clear that the survey methods were having an adverse effect on the eagles, but the majority of the nests had failed by this point.
The data suggest that the approach of the surveyor to the nest had considerable impact on the birds’ breeding success and behaviour. The rate of nest failure from the behavioural study nests was significantly higher than the state-wide nest failure rate in the same year, indicating that disturbance from the study methods increased the likelihood of nest failure. There is likely some inflation of the estimate of breeding failure state-wide due to the presence of ‘maintained’ nests, but this would decrease the significant difference between the behavioural study nests and the overall nests for 2013. Thus, the failure rate of the behavioural study nests was conclusively higher than expected. Therefore, disturbance from the behavioural study methods influenced the breeding outcome.

This study confirmed that eagles are very sensitive to disturbance during breeding, but there is some difference between nests. While eagles mostly flushed from the nest as we approached the hides, the time for eagles to return to each nest after flushing was highly variable. Two eagles did not flush during our approach, while others may have flushed for more than an hour during the first visit. This reduction in nest attentiveness can have detrimental effects on chick health, resulting in prolonged incubation periods (Lyon & Montgomery 1985; Nilsson & Henrik 1988), reduced offspring condition (Ardia, Perez & Clotfelter 2010), or nest failure due to embryonic death or nest predation. Prolonged incubations can result in later hatch dates and thus disadvantage breeding adults as well as chicks by increasing breeding costs (Hansson et al. 2005; Steenhof & Newton 2007). Thus it is likely that the behavioural responses to the seemingly minor (Mooney & Holdsworth 1991) disturbance of humans walking 100-200 m from the nest adversely affected nest success at the study sites.

While it is commonly suggested that raptors can habituate to repeated disturbance (González et al. 2006a; Bejder et al. 2009; Strasser & Heath 2013), behavioural responses of wedge-tailed eagles from this study support sensitisation rather than habituation. The increased time to return to the nests after repeated disturbance supports the hypothesis of Steidl and Anthony (2000), which postulates that frequent short-lasting disturbances (e.g. surveyors approaching the hides) within the same breeding territory could have cumulative effects on adult behaviour and result in energetic consequences to offspring.
Assessing the impacts of human activity on raptor behaviour is useful to gauge more subtle impacts than simply monitoring breeding outcomes. Though behavioural surveys are difficult and time-consuming, they give a more detailed picture of how changes in biologically meaningful behaviours at an individual level can result in lower fitness of adults and offspring. Examples of detrimental behavioural changes include lower frequencies of prey deliveries to nests, changed responses to environmental variables (Steidl & Anthony 2000), and higher chances of egg cooling resulting in longer incubation or embryonic failure (Martin et al. 2007). If disturbances persist and the population consists of a high proportion of sensitive eagles, then the accumulation of the effects of disturbance could have detrimental long-term consequences to populations, particularly for long-lived species such as eagles.

Areas for further research

To gain a better understanding of the timing of the breeding season, factors that affect nest success, and the breeding behaviour of the Tasmanian wedge-tailed eagle, further behavioural surveys along with state-wide nest surveys are needed. The best technique to obtain behavioural data from the nests of such a sensitive raptor species is using remote video cameras, set up prior to the onset of incubation (Rogers 2005; Delaney et al. 2011). Though there are considerable upfront costs to this approach, the data collected from even a small number of cameras over a few breeding seasons would help provide answers many of the questions raised by this study while minimising disturbance and limiting the bias that direct observation techniques create (Booms & Fuller 2003; Delaney et al. 2011).

Using cameras that acquired data from the entire breeding season could help determine the true start date of incubation and confirm the length of breeding stages. This would remove the bias present in the current timing data, which bases the timing of the breeding season solely on successful nests. The onset of incubation can easily be detected on video, either based on presence of eggs or behavioural changes (Debus et al. 2007). The length of each period of the breeding season used to determine the onset of incubation for this study was based on findings from a behavioural study at three Aquila audax audax nests (Debus et al. 2007). However, as there can be intraspecific variation in the timing of breeding periods, notably prolonged incubation due to egg cooling in colder parts of a species’ geographic range (Nilsson & Henrik 1988; Olson, Vleck &
Vleck 2006), data collected using video surveillance would help determine if the incubation period estimate is accurate for Tasmanian wedge-tailed eagles.

The influence of weather on wedge-tailed eagles’ breeding behaviour and responses to disturbance is another area requiring further research. Breeding behaviour can be affected by weather, with more inclement weather corresponding to increased nest attendance and an observed tolerance to human disturbance (Beer 1961; Afton 1980). This increased nest attendance is likely to prevent exposure of eggs during cold, wet weather to limit egg cooling and reduce the risk of microbial infection, a risk mitigated by incubation and increased by moisture (D’Alba, Oborn & Shawkey 2010). Further studies are necessary to determine if higher nest attendance and observed tolerance to disturbance in poor weather conditions occurs in Tasmanian wedge-tailed eagles, because the behavioural studies were only conducted on days with good weather to minimise the risk of nest failure if birds were flushed by our approach.

An additional area of research is examining the prevalence of nest predation by corvids, which may pose a greater threat than cooling to exposed eggs or chicks. Nest predation is a common cause for nest failure in other eagle species (Gil-Sanchez et al. 2004). Although nest predation of a Tasmanian wedge-tailed eagle egg by a forest raven (Corvis tasmanicus) was only observed at a single study nest, the relatively low number of observation hours suggest that nest predation could be a prevalent occurrence while adults are off the nest, particularly since the raven was able to extract the chick from the egg within eight minutes from the eagle leaving the nest. As human presence can attract corvids to nests and increase likelihood of nest predation (Strang 1980; Ibanez-Alamo, Santllorente & Soler 2012), the high sensitivity of wedge-tailed eagles to humans may put them at high risk of egg predation. Additionally, nest predation by corvids has been shown to increase in forest fragments close to forest-farmland edges (Andrén 1992), and many wedge-tailed eagle nests are located forest fragments adjacent to agricultural land (Koch, Wiersma & Munks 2012).

**Synthesis**

Biotic and abiotic factors can affect the timing of the breeding season and the likelihood of breeding success in the Tasmanian wedge-tailed eagle on both an individual and population level. Increased spring rainfall corresponded to delayed breeding seasons
and lower nest success. Colder winter temperatures corresponded to delayed breeding times, but was not related to the likelihood of breeding success. Despite expectations developed from studies of other raptors, there was no evidence for a relationship between prey abundance and the timing of the breeding season or likelihood of nest success for the Tasmanian wedge-tailed eagle. On an individual nest level, high nest density within a territory, which is hypothesised to increase with levels of disturbance in the territory, was associated with the lower nest success. Disturbance, particularly in the form of pedestrian activity in close proximity to nests (100-200 m away) during the breeding season often resulted in eagles flushing from the nest, leaving eggs and chicks exposed and increasing the likelihood of nest failure at an individual nest level. Though pedestrian activity was highly disturbing in close proximity to nests, road density near nests was not found to influence breeding success. However, the impact of prey and road density on breeding could be re-examined if more detailed and fine-scale data sets become available, such as prey abundances within breeding territories during the winter and spring or examining road usage rather than just the existence of roads. As the timing of the breeding season has been determined retrospectively by chick age, a more accurate determination of the onset of incubation and the length of each breeding phase in Tasmanian wedge-tailed eagles, would enable confirmation of the findings regarding the timing of the breeding season.

The breeding success of the Tasmanian wedge-tailed eagle is of high conservation concern, as it is essential for maintaining a stable population. Results from this study confirmed the long-standing hypothesis that Tasmanian wedge-tailed eagles are extremely sensitive to disturbance, and their behavioural responses to human activity in close proximity to the nest increase the likelihood of nest failure. This study highlighted the influence of rainfall, temperature, and human influence on the breeding timing, success and behaviour of the subspecies. However, as detailed above, further research is essential to provide a deeper understanding of the sensitive nature of these eagles and how human influence can be mitigated.
5. References


Appendix 1. Coefficients, AIC values, and Akaike weights for complete set of candidate models of wedge-tailed eagle nest productivity. Random effects NestID and Year are included in all models.

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