The effects of ambient temperature and rainfall on the clutch initiation, egg mass and clutch size in the European starling (*Sturnus vulgaris*)

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Abstract

Climate change is an ongoing global phenomenon resulting in elevated temperatures and more intense rainfall events. These changes in temperature and rainfall have affected the breeding behaviour of many avian species. The purpose of this study is to examine the effects of ambient temperature and rainfall on clutch initiation date, egg mass, and clutch size in European starlings (*Sturnus vulgaris*). I predicted that starlings would initiate clutches earlier with increases in temperature and rainfall. I also predicted that increases in temperature and rainfall would result in higher egg mass and clutch sizes. A free-living colony was studied from 2007-2009 and 2011-2014 for clutch initiation date and clutch size (n = 191 clutches), while egg mass was determined in 2013 and 2014 (n = 76 clutches). There was no effect of mean ambient temperature or mean rainfall on clutch initiation in the European starling over the seven years of data. There was no significant difference between egg mass and mean ambient temperature or mean rainfall; however, first-laid eggs were significantly heavier than last-laid eggs. Contrary to my prediction, clutch size decreased with increases in temperature and showed no correlation with rainfall. The negative correlation between clutch size and ambient temperature is evidence of a seasonal decline, a common phenomenon in birds. This is likely due to a decrease in female condition over the breeding season. It is likely that the breeding behaviour of starlings is controlled by a variety of external and internal cues.

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Introduction

Climate change is an ongoing global phenomenon characterized by extreme weather events and an increase in the Earth's surface air temperature (e.g. Pittock 2009). It is caused by the anthropogenic release of greenhouse gases, such as CO_2 and CH_4, into the atmosphere (IPCC 2007; Pittock 2009). Once in the atmosphere, these gases act as a blanket absorbing heat radiation, resulting in an increase in the Earth's surface temperature by 0.74 ± 0.18°C since the start of the 20th century (Pittock 2009). The increased heating induces higher evaporation and thus faster drying of the ground, which leads to longer and more intense droughts (Trenberth 2011). Water holding capacity of the air increases with temperature, resulting in more intense rainfall events (Trenberth 2011).

Both ambient temperature and precipitation (rainfall) amount affect the reproductive success of birds. Increases in ambient temperature have resulted in earlier nest initiation and egg laying in birds (e.g. Both and te Marvelde 2007; Crick and Sparks 1999; Dunn and Winkler 1999). Earlier laying can be beneficial as it provides birds with an opportunity to have a second brood in the same breeding season and thus, more offspring (Winkel and Hudde 1997). Earlier clutches have significantly more eggs than those laid later in the season (Perrins 1970; Price and Liou 1989; Sydeman et al. 1991; Winkler and Allen 1996). Eggs that are laid earlier will hatch earlier, granting offspring more time before winter to gain foraging experience and energy (e.g. Crick et al. 1997; Winkler and Allen 1996). Temperature also affects the metabolic demand required for egg laying (Meijer et al. 1999). Less energy is required for thermoregulation at warmer temperatures, so more energy can be allocated towards egg formation (Meijer et al.

1999), which is extremely costly (Birkhead and Nettleship 1982). There is also evidence that shows temperature affects avian gonadal growth (Jones 1986; Lewis and Farner 1973; Silverin and Viebke 1994). Warmer temperatures result in faster maturation of the testes, permitting males to mate earlier.

Temperature also has an effect on avian food availability (Winkler et al. 2013). Many avian species will lay earlier to synchronize the hatching of their eggs with peak food availability, thereby increasing fledgling success (Barrientos et al. 2007; Daan et al. 1989; Dunn 2004; Vedder 2012). Källander and Karlsson (1993) confirmed that increased food results in earlier clutch initiation in European starlings (*Sturnus vulgaris*) by supplemental feeding experiments. Aerial insectivores, such as tree swallows (*Tachycineta bicolor*), are particularly affected by ambient temperature because aerial insect abundance correlates positively with ambient temperature (Taylor 1963; Winkler et al. 2013). Insects in Ithaca, New York, required a temperature of at least 18.5ºC for flight activity (Winkler et al. 2013). For ground-foraging European starlings in Aberdeen, UK, leatherjackets (*Tipula* sp. Larvae), a soil-living invertebrate, make up 80% of their diet (Dunnet 1955). Increased soil temperature results in greater growth of leatherjackets (Dunnet 1955). Earthworms (*Lumbricus terrestris*) are a common food source for many birds such as European starlings and American robins (*Turdus migratorius*); they develop slower at low temperatures (10ºC) (Berry & Jordan 2001) and die at temperatures above 25ºC (Berry and Jordan 2001; Khan et al. 2012). Dark eyed juncos (*Junco hyemalis*) are granivores that commonly feed on buckwheat seeds. Buckwheat develops much faster in higher temperatures, but also perishes sooner (Hall 1950; Michiyama and Sakurai 1999). Temperatures that are too low delay the development of seeds considerably (Hall 1950).

Some birds are long-distance migrants and cannot correlate their arrival dates with peak food availability, known as the mismatch hypothesis (Both and Visser 2001; Visser et al. 1998). For example, an increase in temperatures in the Netherlands has advanced the timing of peak insect availability (Harrington et al. 1999). For the pied flycatcher (*Ficedula hypoleuca*), an insectivorous bird, this is detrimental as they arrive to the Netherlands too late to time their laying with this peak food availability (Both and Visser 2001).

Rainfall is also important in the growth and abundance of vegetation for granivorous birds (Boag & Grant 1984; Dunning & Brown 1982; Grant & Grant 1980; Pulliam & Brand 1975). General insect abundance increases with rainfall (Tanaka and Tanaka 1982) through an increase in plant resources as insect food (Wolda 1978). General insect abundance and biomass increase with rainfall (Tanaka & Tanaka 1982). Earthworms are sensitive to soil moisture and are most abundant during the wettest months (Eggleton et al. 2009). As all these factors increase with rainfall, many avian species are likely to initiate egg laying earlier so their offspring can hatch during peak food availability.

Reproductive success may also be increased by increasing egg mass. Heavier eggs have a greater likelihood of hatching (Potti 2008; Saino et al. 2004) and contain heavier nestlings which increases nestling survival (Arnold et al. 2006; Smith and Bruun 1998; Strysky et al. 1999). Heavier nestlings are also more likely to have higher fitness at fledging and increased juvenile survival than lighter offspring (Smith and Bruun 1998; Styrsky et al. 1999). Most of the effects of temperature, rainfall and food availability on egg mass occur during the period of rapid yolk development (RYD) (Ardia et al. 2006;

Saino et al. 2004), which is 5-6 days for most passerines (Ardia et al. 2006; Navara et al. 2006). RYD marks the start of egg formation (Ardia et al. 2006). Therefore, any effects on egg quality must occur during this time period (Ardia et al. 2006). During RYD, lipoproteins are deposited into the yolk of developing follicles (Astheimer 1986; Durant et al. 2004). Higher temperatures during the RYD period increase egg mass (Saino et al. 2004; Stevenson and Bryant 2000). Since egg production is a costly procedure (Birkhead and Nettleship 1982), birds can use more resources to create heavier eggs during higher temperatures (Pendlebury and Bryant 2005; Stevenson and Bryant 2000). Heavier eggs could be a result of increased food availability or lower thermoregulation requirements (Pendlebury and Bryant 2005; Stevenson and Bryant 2000). As rainfall also increases food availability, it is likely that increased rainfall in the 5-6 days prior to laying would also increase egg mass.

Clutch size in birds is constrained by the parents' ability to provide enough food to their offspring (Lack 1954, 1966; Sanz and Moreno 1995). Females will lay clutch sizes that maximize the number of surviving offspring (Lack 1947; Pettifor 1993). For most birds, there is no direct correlation of temperature and rainfall on clutch size (Torti and Dunn 2005). However, increases in food availability allow birds to lay more eggs (Hiom et al. 1991; Högstedt 1981; Pendlebury and Bryant 2005; Sanz and Moreno 1995). Therefore, as food availability increases with temperature and rainfall, clutch size should also increase with temperature and rainfall. However, evidence suggests a seasonal decline in clutch size (Christians et al. 2001; Drent and Daan 1980; Newton and Marquiss 1984). Females gather resources at the beginning of the breeding season and gain weight before laying their first clutch (Newton and Marquiss 1984). After losing weight laying their first clutch, females are not capable of gaining the same amount of weight before their second clutch (Newton and Marquiss 1984). Therefore, the seasonal decline in clutch size is likely related to female condition (Christians et al. 2001; Newton and Marquiss 1984).

European starlings are an excellent species with which to examine the effects of ambient temperature and rainfall on different aspects of reproductive behaviour. They have variable clutch sizes, are double-brooded and ground foragers (Kessel 1957). They are semi-colonial cavity nesters that breed in natural holes (cavities) found in trees or telephone poles as well as in artificial cavities such as dryer vents and drainage pipes (Kessel 1957). Males begin searching for a nest site in late winter. Once a suitable site is found, they begin nest formation and mate attraction. Females choose a mate based on their song, nest site (Kessel 1957) or hackles (Barber et al. submitted). After pair formation, the female helps the male complete the nest (Kessel 1957; Royall 1966). Starlings are typically monogamous, but facultative polygyny has been observed in many populations (Kessel 1957; Komdeur et al. 2005; Pinxten et al. 1989). Females lay, on average, 3-6 eggs per clutch and typically have two clutches per year (Crossner 1977; Lack 1948). Both the male and female incubate the eggs, which hatch approximately 12 days after initiation of incubation (Kessel 1957; Royall 1966). Both parents also participate in nestling provisioning (Feare 1984; Pinxten and Eens 1994). Nestlings fledge after a period of 21-23 days in the nest (Kessel 1957).

The purpose of this study was to examine the effects of temperature and rainfall on reproductive effort of female European starlings. My first objective was to examine whether temperature and rainfall affect laying date. By examining date of clutch initiation over seven years, I predicted that starlings would initiate their clutches sooner, with increased ambient temperature and rainfall as indicators for an increase in food availability. My second objective was to determine if average ambient temperature during egg development affects clutch size and egg mass. I predicted that clutch size and egg mass would increase with temperature as food availability should also increase. Finally, my third objective was to investigate if rainfall had any effect on clutch size and egg mass. Since starlings are mainly ground foragers, I expected that increased rainfall would cause an increase in clutch size and egg mass as earthworms and insects increase in abundance during rain events.

Methods

A free-living colony of breeding European starlings was studied at Saint Mary's University in Halifax, Nova Scotia, Canada (44° 37' 54.07″ N, 63° 34' 47.09″ W) for the years 2007-2009 and 2011-2014. Between 40 and 45 wooden nestboxes were attached on trees 3-5 m from the ground throughout the campus (number of nestboxes varied year to year) (Figure 1). Nestboxes were 16cm long x 17.5 cm wide x 42 cm tall with an opening 5 cm in diameter. Nestboxes were checked daily, starting in late April, to determine date of the first egg laid and clutch size (n=191 clutches; Table 1). Starlings lay eggs later in the day than most other passerines, between 0800 and 1000h (Feare 1984), therefore, all nest checks were done after 1100h to ensure females were not disturbed during the egg laying process. In 2013 and 2014, new eggs were weighed to the nearest 0.1g on the date of laying using an AWS-250 digital pocket scale. On windy or rainy days, the entire scale was placed in a box for protection to obtain accurate measurements. The eggs were numbered on their broad end according to laying order, using a permanent, non-toxic marker. Nestboxes were checked every 3 days until close to the point of expected hatch time, where they were checked on a daily basis. To examine the difference in clutch mass between first and second clutches, first clutches were considered those laid before Julian day 28 and second clutches were all those laid from Julian day 28 and later. Julian day 1 signifies April 18. Only data from first time recorded pairs was used.

Mean daily temperatures (ºC) and total precipitation (rainfall; mm) were obtained from the closest Environment Canada weather stations: Shearwater RCS (44° 37' 47.00" N, 63° 30' 48.00" W) and Shearwater Auto (44° 38' 11.00" N, 63° 30' 24.00" W), Nova Scotia, Canada. Mean daily temperatures and mean total rainfall were recorded for six days before laying date to account for rapid yolk deposition (Ardia et al. 2006; Navara et al., 2006).

GraphPad Prism software (version 5.04 for Windows, GraphPad Software, La Jolla California USA, www.graphpad.com) was used for statistical analysis of data. All data was tested for normality using D'Agostino & Pearson omnibus normality test. Temperature and rainfall were each tested for correlation with 1) mean egg mass and 2) clutch size using Spearman rank tests. Unpaired t-tests were conducted to examine the relationship between total clutch mass for first and second clutches and clutch size for first and second clutches. A Wilcoxon matched-pairs signed rank test was used to compare the masses of first and last eggs. Results were considered significant when $P \leq 0.05$.

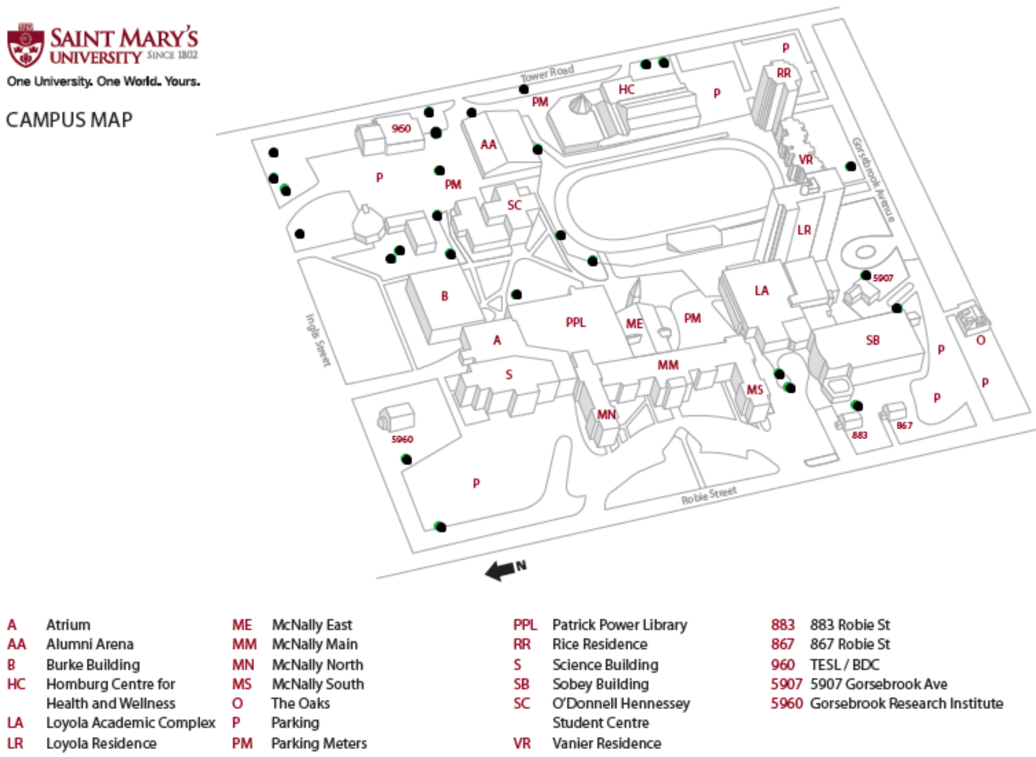

Figure 1. Nestboxes on location of Saint Mary's University campus for 2014, represented by ●

Table 1. Total number of first and second clutches examined from 2007-2009 and 2011-2014

Year	1st clutches	2nd clutches	Total # of clutches
2007	14	6	20
2008	7	2	9
2009	14	8	22
2011	16	5	21
2012	30	14	44
2013	25	25	50
2014	27	-	27

Results

There were 191 clutches monitored for first-time recorded pairs between 2007-2009 and 2011-2014. Clutch initiation was earliest in 2012 and 2008 when the first egg was laid on April 18 and April 20, respectively. The years 2007 and 2009 had the latest clutch initiation dates, with the first eggs being laid on April 26 and 27, respectively.

Total clutch mass for first (2013 and 2014) and second (2013) nests was compared to determine whether it could be pooled across both clutches. However, first clutches were significantly heavier than second clutches ($t = 2.723$, $df = 74$, $P = 0.008$; Figure 5), due to first clutches having significantly more eggs than second clutches ($t = 2.502$, $df = 74$, $P = 0.01$; Figure 6). Therefore, mean egg mass/clutch was instead used to compare egg mass with temperature and rainfall. Similarly, when looking at clutch size over the seven years, first clutches were significantly larger than second clutches ($t = 4.733$, $df = 189$, $P < 0.0001$; Figure 7). No significant difference existed in mean egg mass between first and second clutches ($t = 0.4877$, $df = 74$, $P = 0.63$) and mean egg mass varied between 6.1 and 8.5 grams (Figure 8). Mean egg mass was not associated with mean ambient temperature ($r_s = -0.097$, $n = 76$, $P = 0.4$), nor with mean total rainfall ($r_s = 0.126$, $n = 76$, $P = 0.28$). First-laid eggs in a clutch were significantly heavier than last-laid eggs ($W = -933.0$, $n = 76$, $P = 0.007$; Figure 9).

Clutch size was negatively correlated with mean ambient temperature ($r_s = -0.326$, $n = 191$, $P < 0.0001$); but was not associated with mean total rainfall ($r_s = -0.090$, $n = 191$, $P = 0.21$).

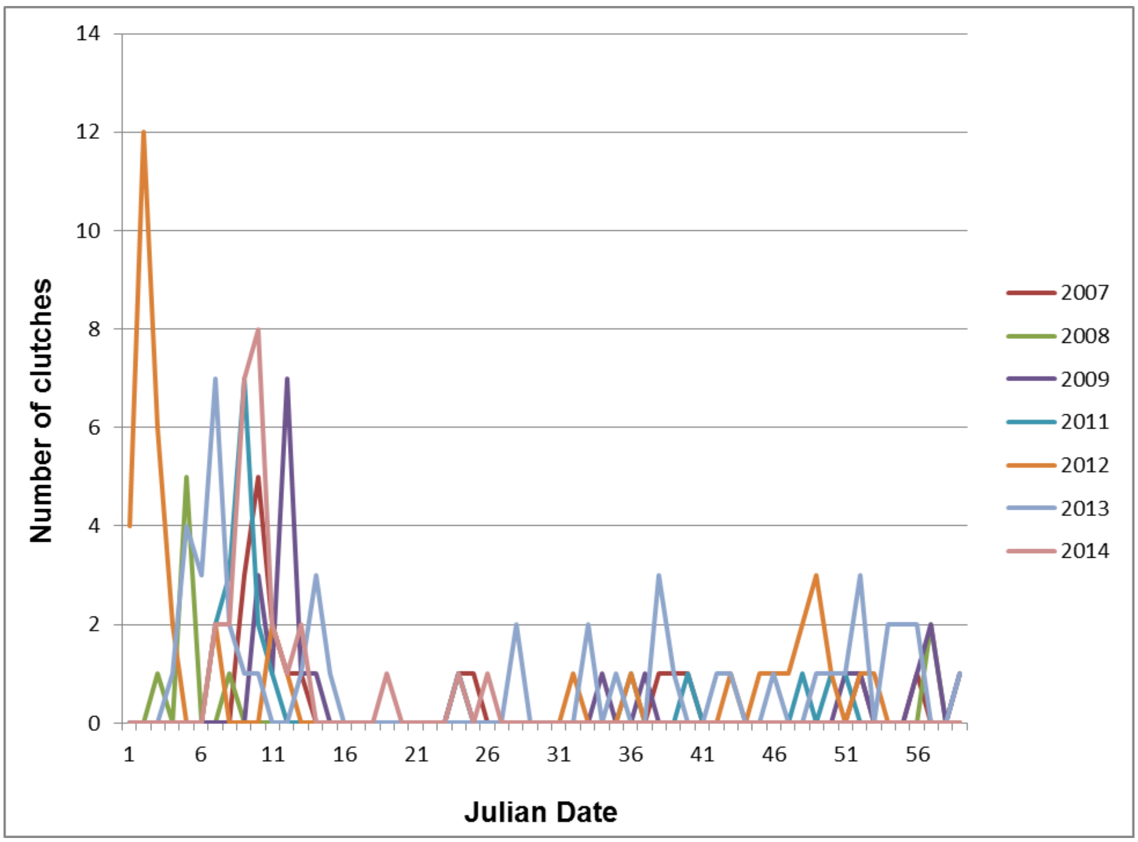

Figure 2. Number of clutches initiated per Julian date over seven years. Julian date 1 represents April 18

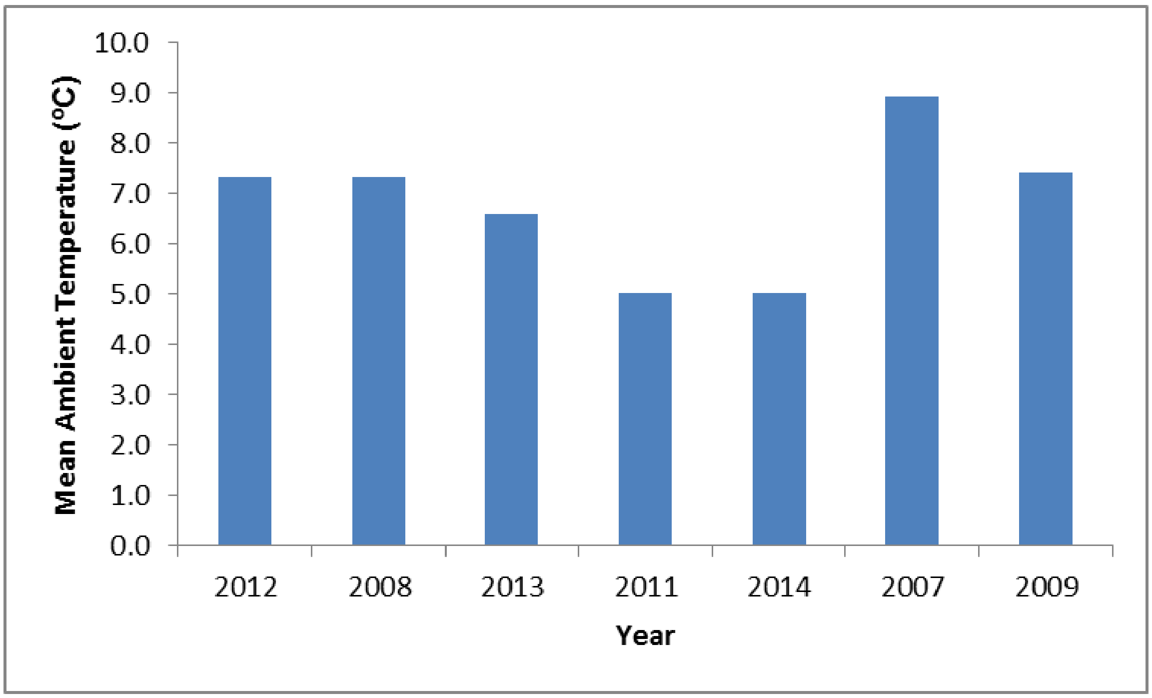

Figure 3. Mean ambient temperature over period of rapid yolk deposition per year in order of earliest laying year to the latest laying year

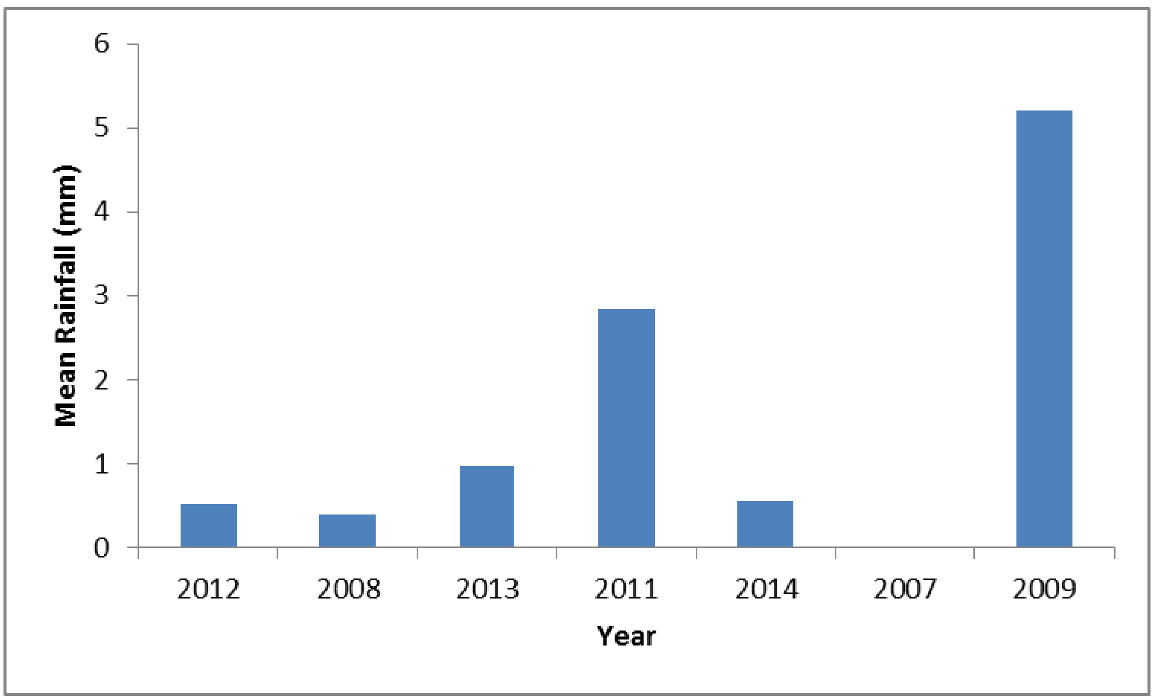

Figure 4. Mean rainfall during the period of rapid yolk development per year in order of earliest laying year to the latest laying year

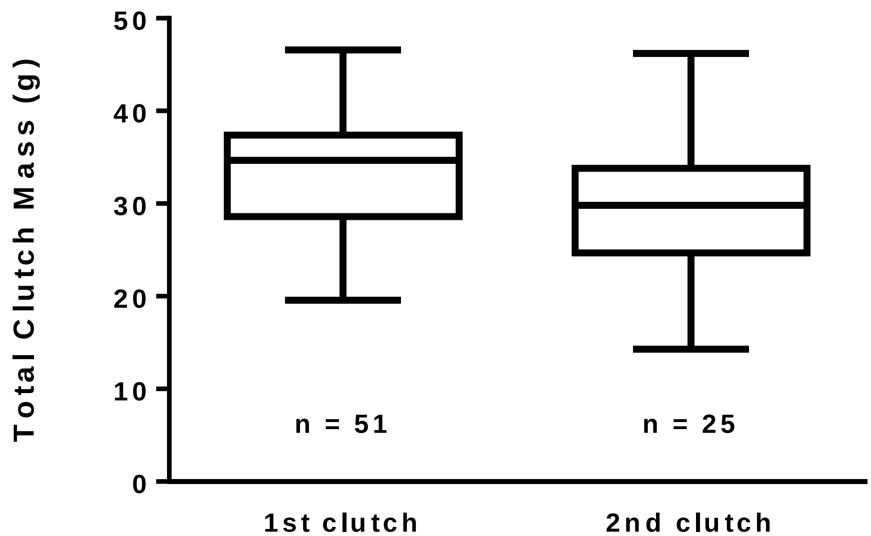

Figure 5. Total clutch mass for first (2013 and 2014) and second (2013) clutches

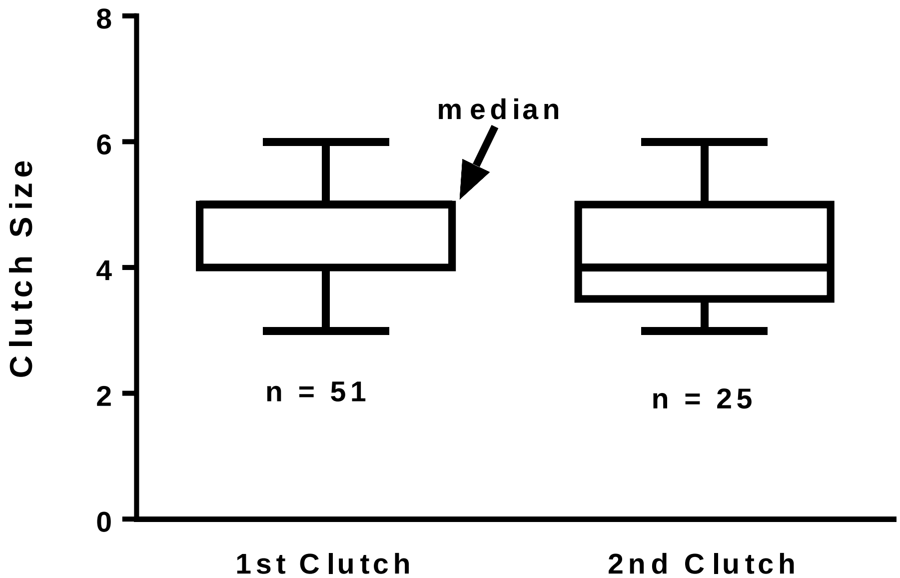

Figure 6. Clutch sizes of first (2013 and 2014) and second nests (2013)

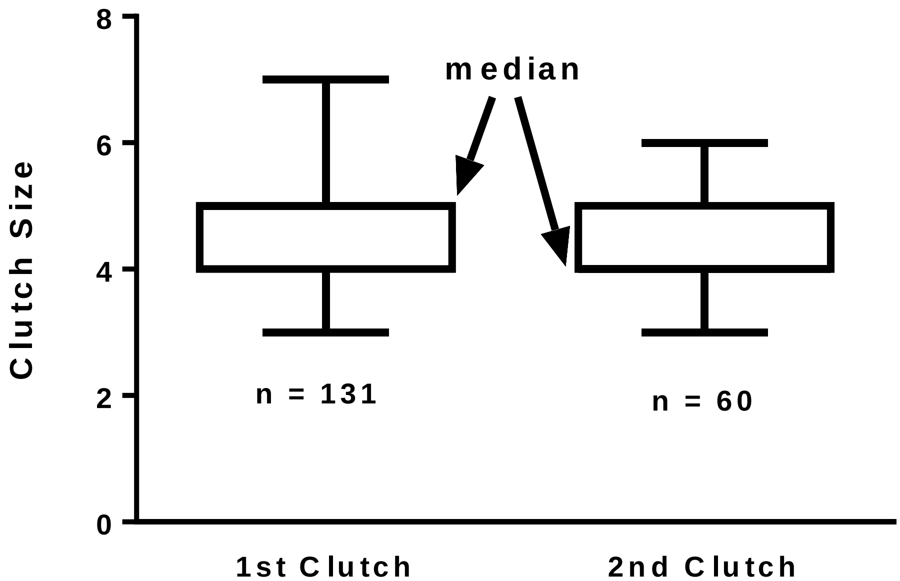

Figure 7. Clutch sizes of first and second nests over seven years

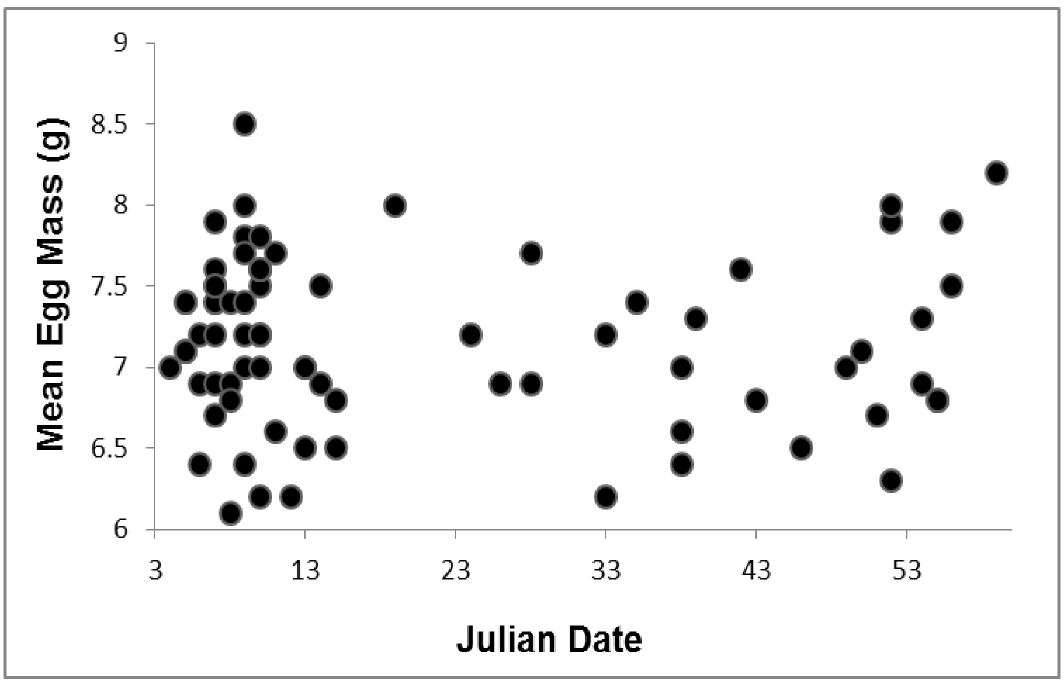

Figure 8. Variation in mean egg mass per nest over the breeding season in 2013 and 2014 (Julian day 3 represents April 20; n = 76)

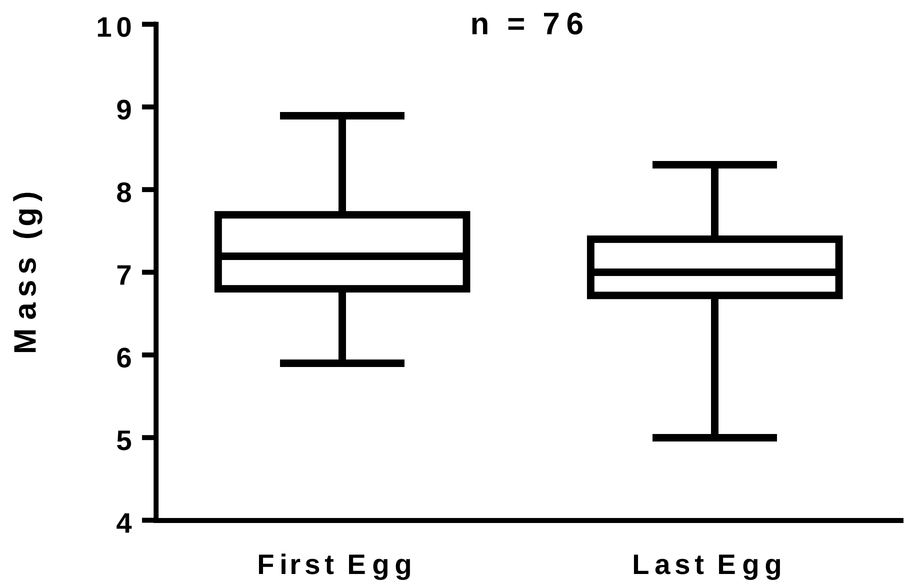

Figure 9. Egg mass for first and last-laid eggs (2013 and 2014)

Discussion

Clutch initiation in the European starling was not affected by temperature and rainfall over the 7 years of data. Figure 3 shows that there is no pattern in clutch initiation with ambient temperature. The year 2007 was the warmest, but also one of the latest years to begin clutch initiation. According to my predictions, 2014 should have been the earliest to begin clutch initiation, but it was still one of the later years to begin clutch initiation. Figure 4 shows a similar lack of pattern in clutch initiation with mean rainfall. It was predicted that increased rainfall would cause the birds to begin clutch initiation earlier. However, 2009 had the highest mean rainfall, but was the latest year to begin clutch initiation. The years 2008 and 2012 were the earliest, but had minimal mean rainfall. Many studies have shown the effects on clutch initiation over a long term period of 20 or more years (e.g. Both and te Marvelde 2007; Crick and Sparks 1999; Dunn and Winkler 1999). Therefore, it is possible that temperature and rainfall may have an effect on clutch initiation in the long term. However, there are no short term effects on clutch initiation. It is also possible that climate change has a larger effect on long distance migrants (Both et al. 2005; Both and Visser 2001). The starling is a resident bird or short distance migrant, much like the great tit (*Parus major*). Over a period of 23 years, there was no advancement in clutch initiation for the great tit (Visser et al. 1998).

It is also possible that clutch initiation is determined by other factors or a combination of external and internal cues. Examples include photoperiod (Dawson et al. 2001; Lambrechts et al. 1997; Tewary and Dixit 1986), snow cover (Hahn et al. 2004; Keppie and Towers 1990; Madsen et al. 2007; Marti 1994), food availability (Daan et al. 1989; Dunn 2004; Källander and Karlsson 1993), female age (Hipfner et al. 1997;

Jarvinen 1991; Spurr and Milne 1976) and female condition (Descamps et al. 2011; Winkler and Allen 1995).

For my study, egg mass did not increase with mean ambient temperature or mean total rainfall. Other studies have also found no correlation between egg mass and ambient temperature (e.g. Ardia et al. 2006; Chausson et al. 2014) or food availability (e.g. Arcese and Smith 1988; Carlson 1989; Horsfall 1984; Nilsson and Svensson 1993). Egg mass may be related to a combination of environmental factors such as food resources and female condition (Ardia et al. 2006; Christians 2002). Female condition has been positively correlated with egg mass in several species (e.g. Leblanc 1989; Strysky et al. 2002; Wiggins 1990) and would be good to examine in European starlings.

There was a significant difference in egg mass between first and last-laid eggs in a clutch with first-laid eggs being significantly heavier. Many conflicting reports exist in the literature with respect to egg mass and laying order. Egg mass increased with laying order in the tree swallow (*Tachycineta bicolor*; Ardia et al. 2006; Zach 1982), Green-rumped parrotlet (*Forpus passerines*; Budden & Beissinger 2005), and Bengalese finch (*Lonchura striata* var. *domestica*; Soma et al. 2007). Egg mass decreased with laying order in the black kite (*Milvus migrans*; Viñuela 1997). Blue-footed boobies (*Sula nebouxii*) had an increase in egg mass with laying order for first clutches, but a decrease with laying order in second clutches (D'Alba and Torres 2007). Because egg mass is variable among species, it is likely that it is dependent on female condition and resources available (Budden & Beissinger 2005; D'Alba and Torres 2007; Kvalnes et al. 2013; Reynolds et al. 2003; Saino et al. 2010; Soma et al. 2007).

Clutch size in European starlings decreased as temperatures increased, and first clutches were significantly larger than second clutches. These two findings are evidence of a seasonal decline in clutch size. One of the possible causes is a seasonal decline in food availability (Newton and Marquiss 1984; Tortosa et al. 2003). Females that lay later in the season have fewer resources available for egg formation (Newton and Marquiss 1984; Tortosa et al. 2003). Another potential factor is that later clutches have a lower reproductive value (Smith 1993; Winkler and Allen 1996), because nestling survival decreases over the breeding season (Daan et al. 1988; Tinbergen and Daan 1990; Young 1994). Females will allocate fewer resources to egg laying and more towards their own survival if offspring survival is lower (Smith 1993; Winkler and Allen 1996). Age of the female also plays a role in the seasonal decline of clutch size. Younger birds tend to lay later and lay smaller clutches (Hochachka 1990; Smith 1993). Older females have more experience and can forage and time their breeding more efficiently than young females (Rowe et al. 1994; Winkler and Allen 1996). Seasonal decline in clutch size has been related to female quality (Christians et al. 2001; Verhulst et al. 1995). After European starlings lay a first clutch, much of their resources are depleted for the production of a second clutch (Christians et al. 2001); therefore, smaller second clutches would be laid to compensate for this loss in resources. Future studies would benefit from comparing clutch size to female condition, as well as quantifying food availability to examine its abundance during the breeding season.

In conclusion, there is no effect of ambient temperature and rainfall on the clutch initiation, egg mass and clutch size of the European starling over a period of seven years. Counter to my predictions, the starlings are not initiating egg laying earlier with increased ambient temperature or rainfall. It is likely that ambient temperature and rainfall are just some of the external cues birds rely on to determine date of laying. Seven years of data may not be enough to reflect the effects of climate change on the breeding behaviour of starlings. This study should continue into the future to obtain long term results. Also counter to my predictions, there was a seasonal decline in clutch size. The was also no effect of rainfall on clutch size. Ambient temperature and rainfall showed no significant effects on mean egg mass, however, the data suggests that food availability plays an important role in egg mass as first-laid eggs were significantly heavier than last-laid eggs. As a double-brooded bird, European starlings may use many resources for the production of the first clutch with less available for the second clutch. Overall, many factors are involved in the breeding behaviour of the European starling. There are no short term effects of ambient temperature and rainfall on clutch initiation, egg mass and clutch size and this study should continue into the future.

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