

Short communication

A seasonal population matrix model of the Caribbean Red-tailed Hawk *Buteo jamaicensis jamaicensis* in eastern Puerto Rico

 JULIO C. GALLARDO^{1*}  FRANCISCO J. VILELLA² & MICHAEL E. COLVIN¹
¹Department of Wildlife, Fisheries and Aquaculture, Mississippi State University, Mississippi State, MS 39762, USA

²U. S. Geological Survey, Mississippi Cooperative Fish and Wildlife Research Unit, Department of Wildlife, Fisheries and Aquaculture, Mississippi State University, Mississippi State, MS 39762, USA

Reliable estimates of life history parameters and their functional role in animal population trajectories are critical, yet often missing, components in conservation and management. We developed seasonal matrix population models of the Red-tailed Hawk *Buteo jamaicensis jamaicensis* in the upper and lower forests of the Luquillo Mountains, Puerto Rico, to describe the influence of early life stages (nestling and clutch survival) on population growth. Modelled populations exhibited positive discrete rates of growth in forests above 400 m (λ highlands = 1.05) and in forests below 400 m (λ lowlands = 1.27) of the Luquillo Mountains. Further, adult survival was the parameter with the highest proportional effect and direct contribution to growth of the population. Besides survival of adults, our results identified that nestling survival had the second greatest influence on λ , stressing the importance of this life stage for the population growth rate of Red-tailed Hawks in our study area. Seasonal matrices are not commonly used to describe population dynamics of birds. However, these may be a useful tool to analyse the influence of life stages in the annual cycle to better address conservation and management needs, especially for species inhabiting oceanic islands.

Keywords: Caribbean, elasticity analysis, islands, population analysis, seasonal matrix, sensitivity analysis.

*Corresponding author.

Email: jcgallardodelangel@gmail.com

Twitter: @JC_GallardoDA

Animal demography may be influenced by a multitude of factors with consequent effects on population growth (Elton 1924, Nicholson 1933, Andrewartha & Birch 1954, Sæther & Bakke 2000, Coulson *et al.* 2001, Katzner *et al.* 2007). Similar stressors may induce varied responses during different life stages of an organism (Sæther & Bakke 2000, Coulson *et al.* 2001). Consequently, understanding the dynamics of different life stages may be important, particularly for species characterized by closed populations or limited immigration rates, both of which are typical of island species (Manlik *et al.* 2016, McGrady *et al.* 2017). However, information on population dynamics of tropical and insular raptor species is limited (Newton 1979, Sæther & Bakke 2000, Katzner *et al.* 2006).

Early life stages can play an important role in defining the population trajectory of an island colonizer. Populations in the early stages of island colonization may initially exhibit population increases as a result of greater reproduction and survivorship (MacArthur & Wilson 1967, Gotelli 2008). Following successful colonization, some species may evolve particular 'island traits', including altered vital rates, while retaining greater values of adult and juvenile survival (MacArthur & Wilson 1967). Therefore, parameters driving population dynamics on islands may contribute differently to population growth as compared with mainland populations (Newton 1998, Sæther & Bakke 2000, Gotelli 2008).

The life histories of oceanic island species are shaped by selective pressures which may result in adaptations such as niche expansion as a consequence of release from interspecific competition (Crowell 1962, MacArthur *et al.* 1972, Abbott 1980, Baker-Gabb 1986, Blondel 2000). Island species are exposed to local stochastic events (e.g. hurricanes) and/or predation rates that potentially can affect survival, reproduction and population growth at a local scale (Brown 1969, 1995, MacArthur *et al.* 1972, Cody 1985, Newton 1998, Johnson 2007). Along with nest predation, weather is one of the most important factors of nest failure for tropical island raptors, decreasing breeding success (Whitacre & Burnham 2012). The impact of breeding success on population growth of island raptors is poorly known, mostly due to the lack of information about early life stage survival (Klavitter *et al.* 2003).

The Red-tailed Hawk *Buteo jamaicensis* has been well studied in temperate environments, but information is limited from Neotropical populations and oceanic islands. In Puerto Rico, the Caribbean Red-tailed Hawk *B. j. jamaicensis* exhibits typical island traits such as extensive spatial overlap among individual territories and greater population density than its mainland conspecifics (Santana *et al.* 1986, Santana & Temple 1988, Boal *et al.* 2003, Nimitz 2005, Llerandi 2006). Raptors play important roles in oceanic islands, given the absence of native mammalian ground predators. In Puerto Rico,

Red-tailed Hawks consume a wide diversity of prey (Snyder *et al.* 1987, Santana & Temple 1988, White *et al.* 2005, Llerandi 2006), including birds and other raptors (e.g. Puerto Rican Short-eared Owl *Asio flammeus portoricensis*, Puerto Rican Parrot *Amazona vittata*), reptiles (e.g. Puerto Rican Boa *Chilabothrus inornatus*), land crabs *Cardisoma guanhumu* and invasive mammals (e.g. rats *Rattus* spp., small Indian mongoose *Herpestes auropuncatus*).

Matrix population models are used to quantify demographic parameters and assess their functional role in population dynamics (Leslie 1945, Caswell 2001, Beissinger *et al.* 2006). Traditional matrix population model structure commonly describes changes in fixed time periods (e.g. annual changes) but cannot model changes across time periods of varying length (Caswell 2001, Caswell & Shyu 2012). In contrast, seasonal matrix models account for a series of phases or transitions to incorporate variability of vital rates estimated over intervals shorter than 1 year (e.g. incubation) and integrate them in a full annual-cycle population model (Caswell 2001). Therefore, seasonal matrix models can provide new insights to evaluate early life stages of raptor populations (Petty 1992, Taylor 1994, Rohner 1996, Newton 1998).

The Red-tailed Hawk in Puerto Rico is probably the best known tropical island form of this widely distributed species. As such, it provides a good subject to assess the relationship of vital rates to population growth in an insular environment (Santana & Temple 1988, Boal *et al.* 2003, Nimitz 2005, Llerandi 2006, Vilella & Nimitz 2012). Island population traits of the Red-tailed Hawk in Puerto Rico may play an important role in breeding success with a direct impact on population growth. In this study, we predicted changes in population growth and associated vital rates would vary among Red-tailed Hawks at different elevations on the island. We developed a seasonal matrix model to estimate the influence of life stages on the rate of finite population increase (λ) of the Red-tailed Hawk, evaluated how island rates might vary from mainland conspecific populations, and assessed how this informs our understanding of the ecology of island raptors in general.

METHODS

Puerto Rico and its satellite islands (17°45'–18°30'N, 65°45'–67°15'W) represent the smallest and easternmost of the Greater Antilles and have a total land area of 8740 km² (Daly *et al.* 2003). The Luquillo Mountains, located in northeastern Puerto Rico, range in elevation from 0 to 1080 m and have a mean annual precipitation of 200–500 cm, with rainfall generally increasing with elevation (Delannoy 1997, Vilella & Nimitz 2012). The lowland moist forest is characterized by a mosaic of second-growth semi-deciduous forest of different stages, pastures and abandoned crop lands. Lowland moist

forest is found at elevations of 0–400 m, with an average annual precipitation of 100–220 cm. The highland forest (subtropical wet forest and lower montane wet forest) is located above 400 m and annual rainfall averages 200–500 cm. Highland forest is characterized by mature and old second-growth broadleaf tropical forests with a continuous canopy (Ewel & Whitmore 1973). The Luquillo Mountains include the largest remaining areas of primary montane forest in Puerto Rico, El Yunque National Forest (Lugo 1994). However, some portions of the Luquillo Mountains (e.g. lowlands) are highly fragmented and reflect past forest disturbances from agriculture and hurricanes, and increasing human development (Foster *et al.* 1999, Castro-Prieto *et al.* 2017).

The Red-tailed Hawk is a widespread and common raptor in North America and it inhabits a wide variety of open and semi-open habitats (Preston & Beane 1993). In the Neotropics, this species has resident populations in Mexico, Central America and the Caribbean islands (Preston & Beane 1993). In Puerto Rico, the Red-tailed Hawk is found across the island and its density is one of the highest recorded along the species' distribution (Nimitz 2005, Llerandi 2006). Santana and Temple (1988) reported differences in nestling and fledgling survival of Red-tailed Hawks among lowland and higher elevation forests in Puerto Rico. We used demographic information from Nimitz (2005) and Santana and Temple (1988) to develop two periodic matrix models for two Red-tailed Hawk populations, one in the highlands and one in the lowlands of the Luquillo Mountains. Our models included five life history stages, each associated with specific demographic parameters and transition probabilities (Table 1).

We assumed equal sex ratios for our focal population based on previous information of equal ratios for some insular *Buteo* species (Newton 1979, Santana & Temple 1988, Klavitter *et al.* 2003, Woolaver *et al.* 2013). We estimated clutch size (CI) by multiplying the average clutch size in Puerto Rico (2.3 eggs) by 0.5 to account for female-only values (Santana & Temple 1988). Clutch survival (S1) was estimated as the proportion of eggs that hatched. Santana and Temple (1988) reported that Red-tailed Hawk nestling survival averaged 0.7 in the highlands and 1.5 in the lowlands. Therefore, we calculated nestling survival probability (S2) by estimating the percentage of fledglings by clutch size, yielding 0.3 (S2_H) for the highlands and 0.65 (S2_L) in the lowlands. Finally, we used survival probabilities reported by Nimitz (2005) from radiomarked individuals in the Luquillo Mountains for juveniles (0.95), second-year birds and adults (0.97); no sex differences were indicated. We considered these survival probabilities to be identical in the lowlands and highlands.

We described the annual life cycle of the Red-tailed Hawk with a stage-transitional scheme that included both transition probabilities (e.g. egg to nestling, nestling

Table 1. Life stage survival probabilities of Caribbean Red-tailed Hawk (*Buteo jamaicensis jamaicensis*) in Puerto Rico.

| Life stage parameter/Survival probability | Value | References |
|---|-------|---------------------------|
| Adult (Ad), adult survival (S4) | 0.97 | Nimitz (2005) |
| Juvenile survival (Ju), second-year survival (S5) | 0.95 | Nimitz (2005) |
| Clutch survival highlands (S1) | 0.6 | Santana and Temple (1988) |
| Clutch survival lowlands (S1) | 0.78 | Santana and Temple (1988) |
| Nestling survival (Ne), in highlands (S2) | 0.7 | Santana and Temple (1988) |
| Nestling survival (Ne), in lowlands (S2) | 1.5 | Santana and Temple (1988) |
| Fledgling survival (F), in highlands (S3) | 0.3 | Santana and Temple (1988) |
| Fledgling survival (F), in lowlands (S3) | 0.65 | Santana and Temple (1988) |
| Clutch size (Cl) | 1.15 | Santana and Temple (1988) |

to fledgling) and other demographic values (e.g. clutch size, adult survival) into a single transition matrix (Fig. 1) following the breeding phenology reported by Santana and Temple (1988). These included: (1) Transition 1 (laying phase), transition of juveniles to second-year birds (S5) and a breeding period that included adult survival (S4) and clutch size (Cl); (2) Transition 2 (incubation phase), transition through the incubation period and clutch survival (S1); (3) Transition 3 (nestling phase), transition through the nestling stage and nestling survival (S2); and (4) Transition 4 (post-fledgling phase), transition from fledging to juvenile (first-year, S3).

We used permutational eigen decomposition of the transition matrices to calculate elasticity and sensitivity values in each transition matrix to estimate the effects of life stages on the population growth rate (λ) of the Red-tailed Hawk in eastern Puerto Rico (Caswell 2001). Sensitivity is the rate at which λ changes with respect to a change in any of the elements of the matrix, in this case each life stage (Caswell 2001, Stevens 2009). Elasticity (or proportional sensitivity) is defined as the proportional relative contribution of each life stage to λ , where proportional values range from 0.00 (low relative importance) to 1.00 (high relative importance; Caswell 2001).

We reported elasticity values to estimate the proportional effect of each life stage on λ and sensitivity values to identify what life stage most contributed to λ and how susceptible it was to changes in different vital rates (Gotelli 2008). Sensitivity identifies the direct relative contribution of each life stage to λ and how susceptible

it is to changes in different vital rates (Caswell 2001, Gotelli 2008, Stevens 2009). We used the logarithmic equation $r = \ln(\lambda)$ to calculate the intrinsic rate of increase (r) of the Red-tailed Hawk in the highlands and lowlands (Gotelli 2008). Parameter (λ , r) estimates and matrix models were implemented in custom code in program R version 3.2.3 (R Core Team 2014). We did not model the effects of density dependence or environmental or demographic stochasticity on the population.

RESULTS

We found that the survival of the Red-tailed Hawk hinged on the adult life stage, which drove population growth in eastern Puerto Rico. In all transition matrices, adult survival had a greater proportional effect on and direct contribution to Red-tailed Hawk population growth in the lowlands (elasticity = 0.53–0.77 and sensitivity = 0.70–1.01) and highlands (elasticity = 0.73–0.86, sensitivity = 0.78–0.94). However, the effect of proportional change on λ of second-year birds in the highlands, fecundity, clutch survival and nestling survival was the same for each stage (elasticity highlands = 0.14, elasticity lowlands = 0.23) (Table 2). In both highlands and lowlands, adult survival had greater sensitivity values than any other life stage, which explained why λ was more sensitive to changes of this parameter. However, our results suggested that nestling survival was the second most important life stage influencing Red-tailed Hawk population growth in eastern Puerto Rico, with a sensitivity of 0.48 in the highlands and 0.38 in the lowlands. This suggests that the survival of nestlings may be especially susceptible to density-dependent (e.g. nest predation) and density-independent limiting factors (e.g. severe weather events) with a direct effect on populations. In eastern Puerto Rico, our models suggested that Red-tailed Hawk populations had a rate of increase of approximately 5% ($\lambda = 1.05$, $r = 0.05$) in the highlands and 27% in the lowlands ($\lambda = 1.27$, $r = 0.24$).

DISCUSSION

Our results indicated that for Red-tailed Hawks in Puerto Rico, adult survival was the parameter of greatest relative importance in each transition. An alteration of 10% in adult survival will change λ between 5.3 and 7.7% in the lowlands and 7.3 and 8.6% in highlands. Our findings were consistent with those reported for other long-lived birds (including raptors), where adult survival is the most important driver of population dynamics (Sæther & Bakke 2000, Klavitter *et al.* 2003, Katzner *et al.* 2006, Sergio *et al.* 2011). These results suggest that adult survival is a major component regulating Red-tailed Hawk populations in eastern Puerto Rico and a key element for its conservation and management.

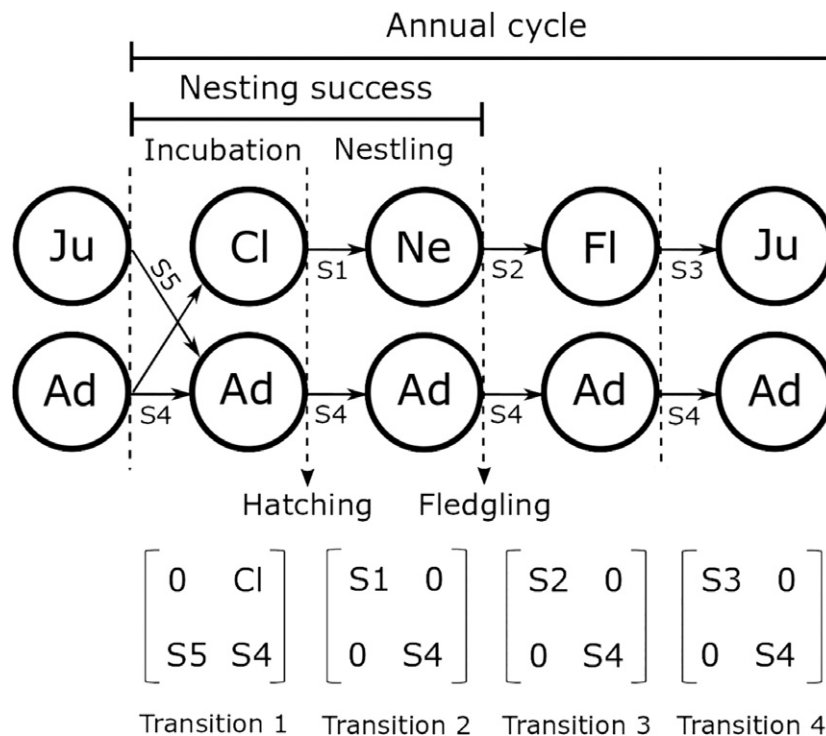


Figure 1. Transition scheme of the annual cycle and projection transition matrices of the Red-tailed Hawk in eastern Puerto Rico. Circles represent clutch size (Cl = 1.15) and four life stages, juvenile (Ju), adults (Ad), nestling (Ne) and fledgling (Fl), arranged in pathways (solid arrows) with their associated survival probabilities, which include: clutch survival in the highlands (S1 = 0.60), clutch survival in the lowlands (S1 = 0.78), nestling survival in the highlands (S2 = 0.30), nestling survival in the lowlands (S2 = 0.60), fledgling/juvenile to 1 year old (S3 = 0.95), adult survival (S4 = 0.97) and second-year bird survival (S5 = 0.97). Clutch size value and each survival probability are arranged in four independent transitions matrices following the annual cycle period of the Red-tailed Hawk: T1, laying phase; T2, incubation phase; T3, nestling phase; T4, post-fledgling phase. Dotted arrows are natural breaks that indicate the beginning and end of a survival probability during the nesting period.

Beyond adult survival, estimates of λ were more sensitive to changes during the nestling stage in both the highlands and the lowlands. Therefore, early life stage transitions may have a greater influence on λ , especially during periods of high mortality or following natural disturbances such as hurricanes (Sergio *et al.* 2011). Breeding success in birds of prey can be particularly vulnerable to weather events that reduce parental care, suppress hunting behaviour or prey availability, and expose nest contents to inclement weather (Elkins 1983, Newton 1998, 2013, Sæther *et al.* 2004, Wilson & Martin 2012). Santana and Temple (1988) reported a reduction in parental care and suppression of hunting behaviour (e.g. increasing nesting mortality) at higher elevations compared to lowlands during periods of high precipitation or prolonged fog. This highlights the importance of adult survival and its link to other sensitive life stages (e.g. nestling survival), especially in stochastic environments.

There is a positive relationship between adult survival and body mass of diurnal birds of prey (Newton *et al.* 2016). The adult survival rate of Red-tailed Hawks in

Puerto Rico is greater (~ 95%) than that of continental *Buteo* hawks with similar body mass (70–88%) but similar to other species of the mainland Neotropics and to other island raptors (Preston & Beane 1993, Kenward *et al.* 2000, Klavitter *et al.* 2003, Nimitz 2005, Schmutz *et al.* 2006, 2008, Rivera-Parra *et al.* 2012, Thorstrom 2012). It is suggested that species of island raptors exhibit higher rates of adult survival than continental forms (Gliwicz 1980, Adler & Levins 1994, Stutchbury & Morton 2001). We could expect this life stage would be of less importance to the mainland population of Red-tailed Hawk as a result of lower adult survival values (80%; Preston & Beane 1993). This marked difference between mainland and island raptors may be a function of the ecological conditions and population traits associated with oceanic insular environments (i.e. ecological release, sedentariness) but this warrants additional study.

A higher rate of annual survival may be linked to life-span, a trait observed in tropical and island species (Snow & Lill 1974, Grant & Grant 1992, Stutchbury & Morton 2001, Klavitter *et al.* 2003, Krüger 2007, Newton *et al.*

Table 2. Sensitivity and elasticity of the different transition matrices during the annual cycle of the Red-tailed Hawk in eastern Puerto Rico.

| Time period | Parameter | Upper forest | | Lowland forest | |
|-------------------------------------|--------------------|--------------|------------|----------------|------------|
| | | Sensitivity | Elasticity | Sensitivity | Elasticity |
| Laying phase (Transition 1) | Clutch size | 0.12 | 0.14 | 0.26 | 0.23 |
| | Juvenile survival | 0.15 | 0.14 | 0.31 | 0.23 |
| | Adult survival | 0.78 | 0.73 | 0.70 | 0.53 |
| Incubation phase (Transition 2) | Clutch survival | 0.24 | 0.14 | 0.38 | 0.23 |
| | Adult survival | 0.93 | 0.86 | 1.01 | 0.77 |
| Nestling phase (Transition 3) | Nestling survival | 0.48 | 0.14 | 0.46 | 0.23 |
| | Adult survival | 0.94 | 0.86 | 1.01 | 0.77 |
| Post-fledgling phase (Transition 4) | Fledgling survival | 0.15 | 0.014 | 0.31 | 0.23 |
| | Adult survival | 0.94 | 0.086 | 1.01 | 0.77 |

2016). Based on our results, we suggest annual survival of adult Red-tailed Hawks and lifespan may have a greater influence on population growth than reproductive success, a pattern previously reported for other raptor species (Sæther & Bakke 2000, Sæther *et al.* 2004, Katzner *et al.* 2006, Krüger 2007, Krüger *et al.* 2010). Our seasonal matrix model suggested greater adult and juvenile survival were important components sustaining population growth of the Red-tailed Hawk in the highlands of eastern Puerto Rico, despite lower reproductive success as reported by Santana and Temple (1988).

Several raptor species in the mainland tropics and islands produce smaller clutches or do not breed every year (Donazar 1990, Simmons 2000, Evans *et al.* 2005). Nevertheless, average clutch size (2.3 eggs) of the Red-tailed Hawk in eastern Puerto Rico was similar to mainland conspecifics, where clutch size average ranges from 2.11 to 2.94 eggs (Santana & Temple 1988, Preston & Beane 1993, Clarkson & Laniawe 2000, Woolaver *et al.* 2014, de Vries 2015). This may partially explain positive modelled population growth rates in eastern Puerto Rico despite lower productivity. The combination of adult and juvenile annual survival and greater number of fledglings may explain the higher sensitivity value of nestling survival in the third transition time in both lowlands and highlands (Table 2), highlighting the importance of this stage in the estimated value of λ for the Red-tailed Hawk in eastern Puerto Rico.

Our results suggest the population of Red-tailed Hawks in eastern Puerto Rico exhibited traits typical of species in the initial phases of island colonization. These are characterized by the early phase of logarithmic population growth driven by high adult survival and reproductive success (MacArthur & Wilson 1967). The long-distance migratory capabilities and demographic traits of the Red-tailed Hawk may have facilitated colonization of most islands of the Greater Antilles (Raffaele *et al.* 1998). In Eurasia, the Common Buzzard *Buteo buteo* has comparable habitat use patterns to the Red-tailed Hawk,

including long-distance migratory populations and insular subspecies (Ferguson-Lees & Christie 2001, Bildstein 2006, Hardey *et al.* 2006). Rodríguez *et al.* (2010) reported that the insular subspecies of the Common Buzzard *B. b. insularum* on the island of Tenerife retains reproductive values similar to the nearest mainland populations but utilizes a wider range of nesting habitats compared with continental populations.

By retaining some mainland traits (e.g. clutch size) and traits typical of tropical islands (e.g. high annual survival), modelled populations of the Red-tailed Hawk in eastern Puerto Rico exhibited sustained population growth in the highlands ($\lambda = 1.05$, $r = 0.05$) and lowlands ($\lambda = 1.27$, $r = 0.24$). However, other factors not accounted for by our model (e.g. gender-specific survival) may also influence Red-tailed Hawk populations in eastern Puerto Rico. Nevertheless, the vital rates estimated may partly explain abundance and spatial patterns of Red-tailed Hawks in the highlands of the Luquillo Mountains (Boal *et al.* 2003, Nimitz 2005, Vilella & Nimitz 2012).

We propose two behavioural non-mutually exclusive hypotheses to explain partially the lower λ values: the individual adjustment hypothesis and the habitat heterogeneity hypothesis. The former argues that the documented greater abundance and spatial overlap might result in increased agonistic interactions among neighbouring Red-tailed Hawks, resulting in individuals displaced to areas of reduced habitat quality and a consequent reduction in overall breeding success and reduced population growth in a specific area (Ferrer & Donazar 1996). The latter hypothesis would address the establishment of a hierarchy, whereby the use of low-quality territories would result in reduced breeding success (Rodenhouse *et al.* 1997). Therefore, we suggest that (1) the highlands of the Luquillo Mountains may represent low-quality breeding habitat given extended periods of severe weather and consequent negative impact on local population growth and (2) the

importance of adult survival may increase with environmental stochasticity.

Matrix algebra has been widely used to describe the dynamics of wild populations, including raptors (Klavitter *et al.* 2003, Krüger 2007). However, the most widely used approaches (e.g. Leslie matrix) are unable to account for the contribution of early life stages to population growth. Seasonal matrix models can be a useful tool to explore the importance of early life stages on the dynamics of insular populations. Further, seasonal models may be useful to illustrate early life stages that may require conservation management measures (Caswell 2001, Davis *et al.* 2004, Westernman *et al.* 2005, Bacaër 2009, Jenouvrier *et al.* 2010, Caswell & Shyu 2012). This modelling approach can be adapted to other island raptors with alternative breeding strategies such as the polyandrous Galapagos Hawk *Buteo galapagoensis* or the Hawaiian Hawk *Buteo solitarius*, a species that breed in alternate years and lay a single egg per breeding attempt. For these island raptors, early life stages may play a major role in their population dynamics that may be overlooked using other population modelling approaches (Clarkson & Laniawe 2000, Hostetler *et al.* 2015).

Hurricanes are the most important source of natural perturbation in the Caribbean, influencing vegetation succession and resulting in potentially long-lasting effects on the population dynamics of island vertebrates (Boose *et al.* 2004, Flynn *et al.* 2010, Wunderle & Arendt 2011). These disturbance events alter forest structure and increase forest openings, benefitting the foraging success of Red-tailed Hawks while increasing the exposure of avian species dependent on closed canopy forest (e.g. Puerto Rican Parrot) to predation (Snyder *et al.* 1987, Brokaw & Walker 1991, Beissinger *et al.* 2008). Overall, our results suggest the landscape of eastern Puerto Rico may promote favourable conditions for high reproductive and survival rates that partially explain the stable population growth of the Red-tailed Hawk. On the other hand, high reproductive and survival rates might be part of the adaptations to sustain stable population growth in island environments subject to periodic stochastic events such as hurricanes. Further research is needed to assess the effect of stochastic events on population dynamics as a part of the process of successful island colonization.

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