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Breeding performance of Crested Goshawk *Accipiter trivirgatus* in urban and rural environments of Taiwan

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Capsule A Crested Goshawk population recently colonizing an urban area of Taiwan is characterized by earlier egg-laying dates, a higher ratio of mixed-age pairs and higher nesting success.
Aims To compare breeding time, productivity and pairing pattern of Crested Goshawk populations between urban and rural areas.
Methods A total of 117 nests, comprising 49 rural and 68 urban ones, were monitored in Taichung, central Taiwan over six years. Age of parents, egg-laying date, clutch size and number of fledglings were recorded from each nest.
Results The urban Crested Goshawk bred 34 days earlier on average than the rural population with a significantly higher nesting success. Mixed-age pairs occurred in a higher frequency in urban (30.9%) than in rural (14.3%) areas. Predation (55.6%) and inclement weather (27.8%) were the two main factors causing nesting failures in rural areas, whereas neither occurred in the urban area.
Conclusion We conclude that the urban Crested Goshawk population benefits from high food supply and low predation risk. The year-round abundance of prey might increase the breeding success of young adults and advance their breeding schedule, which coincidently shifts the brooding period away from the heavy rainy season.

The impact of urbanization on wildlife is an ecological concern of great interest to ecologists in recent years. In most cases, native animals suffer from decreases in the size of original habitats and increase in fragmentation in urban environments. Both factors usually decrease population size and sometimes lead to local extinction (Blair & Johnson 2008, Chamberlain *et al.* 2009). Nevertheless, some birds (e.g. House Sparrows *Passer domesticus*, Rock Doves *Columba livia* and Common Starlings *Sturnus vulgaris*) can effectively adapt to urban ecosystems and produce huge population sizes. Adaptation of these birds in behaviour and breeding strategies has been widely discussed in recent years (Chace & Walsh 2006, Lepczyk & Warren 2012, Møller & Ibáñez-Álamo 2012).

Most raptors occupy the top level of trophic webs and are extremely sensitive to habitat quality (Newton 1979). Highly fragmented habitats, human activity and the change of prey item composition are all critical factors that may restrict some raptors from occupying urban areas (Berry *et al.* 1998). However, some other raptors respond well to urban environment because of the large biomass of suitable prey items such as small birds or squirrels. Cases of urbanized raptors include Cooper's Hawks *Accipiter cooperii*, Sharp-shinned Hawks *A. striatus*, Merlins *Falco columbarius*, and Tawny Owls *Strix aluco* (Warkentin *et al.* 1992, Coleman *et al.* 2002, Stout *et al.* 2007, Solonen & af Ursin 2008). In some of the cases, availability of prey items might be the major reason for their colonization of towns and cities (Warkentin *et al.* 1992, Solonen & af Ursin 2008, Kumar *et al.* 2014).

The urban environment not only affects prey abundance, but also alters avian behaviour, such as flight distance upon disturbance (Møller 2008), escape behaviour (Møller & Ibáñez-Álamo 2012), or daily activity patterns (Huang *et al.* 2006). Urban areas may also affect population characteristics such as the typical age-ratio and the age structure of the breeding population because they represent a new and low-density area during colonization. Generally, mature

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individuals prefer to mate with other adults or individuals of similar age because higher reproductive success is achieved with more experienced mates (Bradley *et al.* 1995, Pärt 2001, Reid *et al.* 2003). In raptors, territory occupancy, nest construction, food supply, and parental care all depend on experience, and making the age of mates crucial for mate choice (Warkentin *et al.* 1992, Ferrer & Penteriani 2003), resulting in age-assortative mating. This behaviour might be especially beneficial for some large-sized raptors with monogamous mating systems and long life spans (Emlen & Oring 1977). In urban areas this may be much less the case because of the availability of vacant territories and differing mortality rates. For example, urban areas provide an environment where food resources, breeding sites, and predator density may vary from typical rural values. These factors may increase the number of vacancies which may facilitate breeding success of pairings of young birds or the formation of mixed-age pairs (Newton 1992).

Adaptations of raptors to urban areas are much less studied in subtropical or tropical regions than those in temperate regions. Taiwan is a subtropical island with an area of only 36 000 km^2, and the total human population was 23 million at the end of 2013. The human density on the island is over 645 people/km^2, while the density in the major cities on the island has exceeded 20 000 people/km^2 (> 40 000 people/km^2 in an extreme case in Yonghe District, New Taipei City). With rapid growth of the population and intense economic development, urbanized areas have expanded rapidly in Taiwan, and the lowlands have been widely occupied by humans. Such extreme urbanization provides a great opportunity to understand how wildlife adapt or avoid such anthropogenic environments (Chace & Walsh 2006).

The Crested Goshawk *Accipiter trivirgatus formosae* is an endemic subspecies in Taiwan and mainly inhabits woodland areas. Among the seven breeding Accipitridae in Taiwan, the Crested Goshawk is the only species that has recently colonized some cities. The process of its urbanization was carefully recorded by bird watchers and could be traced back to the early 2000s. For example, a thorough survey in Taichung City from 1999 to 2000 showed the absence of the Crested Goshawk during this period (Taichung Bird Watching Association 2000, Hu 2008, Severinghaus *et al.* 2012). However, orphan nestlings were first recorded in 2003, and since then, nesting behaviour, injured individuals, and orphan young have been increasingly recorded.

In this study, we aim to (1) evaluate and compare the phenology and productivity of Crested Goshawks between urban and rural areas and investigate the factors that affect nest success; (2) investigate whether the pairing pattern in urban areas is different from rural areas; and (3) compare productivity of adult pairs or mixed-age pairs between urban and rural areas.

METHODS

Study area

Our study sites were located in Taichung (24°09'N, 120° 40'E), western Taiwan. We selected the city centre and countryside around the city as our urban and rural areas, respectively. Human population in this city is approximately 1.1 million people (13 051 people/km^2). Man-made structures (e.g. buildings and roads) occupy 88% of land area, while urban parks, school yards, rivers, and abandoned agricultural areas compose the other 12%. Our rural study site had a human population density of about 1875 person/km^2. In this site, man-made structures occupied only 8% of the land area. Agriculture is the main type of land use, including rice farms, orchards, artificial woodlands, natural woodlands, and rivers, which compose the other 92% of rural land area use.

Pairing pattern

Nesting pairs are categorized into adult pairs and mixed-age pairs in this study. An adult pair means that both mates exhibit definitive adult plumage being greyer on the back of the body, orange-brown on the breast and with dark brown stripes on the belly (Brazil 2009). According to our hand reared orphan nestlings, definitive adult plumage of the Crested Goshawk is acquired at least three years after hatching. A mixed-age pair means that at least one individual within the pair exhibited sub-adult plumage: brownish on the back, and dark brown stripes on the breast and belly (Brazil 2009).

Nest search and nesting phenology

Sex of the parents was determined by the prominent difference in size such that females are always the larger one in a pair (Severinghaus *et al.* 2012). We determined possible nesting sites of the Crested Goshawk by searching for displaying pairs (e.g. exaggerated flapping flight with calling by males) or nest construction behaviour (e.g. twig carrying by both mates). Once the location of the nests was confirmed, we recorded the clutch and brood size either by direct observation from adjacent tall buildings or by a video camera attached to a telescopic aluminium pole with a mobile monitor. We visited each nest every day until nestlings fledged or nesting failure. The reason for nesting failure was recorded in as much detail as possible. For the nests where the egg-laying date was not directly observed, a backdating method was applied to estimate the egg-laying date after the nestlings hatched. An incubation period of 35 days was applied in the backdating estimation as referred to our previous study (Lin *et al.* 2008). We define fledgling as the nestling reaching 48 days old, when the young typically leave and stand outside the nest (Lin *et al.* 2008). A nest with at least one fledgling was defined as a nesting success (Coleman *et al.* 2002, Rosenfield *et al.* 2007, Steenhof & Newton 2007).

Statistical analysis

In order to test the difference of breeding performance of Crested Goshawk between urban and rural areas, we used generalized linear mixed models (GLMM) to compare the breeding phenology, pairing pattern, reproductive success between urban and rural populations including year as a random factor (year was also included as a random factor in all models below). In the analysis of breeding phenology, Julian date was used as response variable with breeding location, pairing pattern and their interaction as predictor variables to test the influence of the urban environment and pairing pattern on breeding phenology. When analysing pairing pattern we used pairing pattern as a binomial response variable with location as predictor variable to test whether the proportion of adult pairs/mixed-age pairs differs or not between urban and rural populations. In the analysis of breeding success, clutch size, number of hatchings, and number of fledglings were used as continuous variables, while the probability that at least one egg successfully hatched, the probability that at least one hatchling fledged in the successfully hatched nests, and the probability that at least one hatchling fledged in all nests were used as nominal variables to denote incubation success, brooding success, and total nesting success, respectively. These variables were used as response variables to build the GLMM models with location, pairing pattern, and their interaction as predictors for understanding how breeding success depended on breeding location. When considering the influence of phenology on breeding success, Julian date was used as a covariate. All statistical analyses were conducted by using SAS 9.4.

RESULTS

Laying date and sub-adult breeding between rural and urban habitats

A total of 117 nesting attempts of the Crested Goshawk were recorded during 2006–11 including 68 urban and 49 rural nests. Breeding phenology differed between the urban and rural population, but was not influenced by pairing pattern. Only breeding location was significant in the GLMM analysis which included year as a random factor (GLMM, habitat: $F_{1,108} = 87.1$, $P < 0.0001$, pairing pattern: $F_{1,108} = 0.01$, $P = 0.93$; habitat*pairing pattern: $F_{1,108} = 0.04$, $P = 0.83$). The mean egg-laying date of the urban Crested Goshawk is 1st March (60.73 ± 2.63 Julian date), which was significantly earlier than that of their rural counterparts, 4th April (94.22 ± 3.50 Julian date) (Fig. 1).

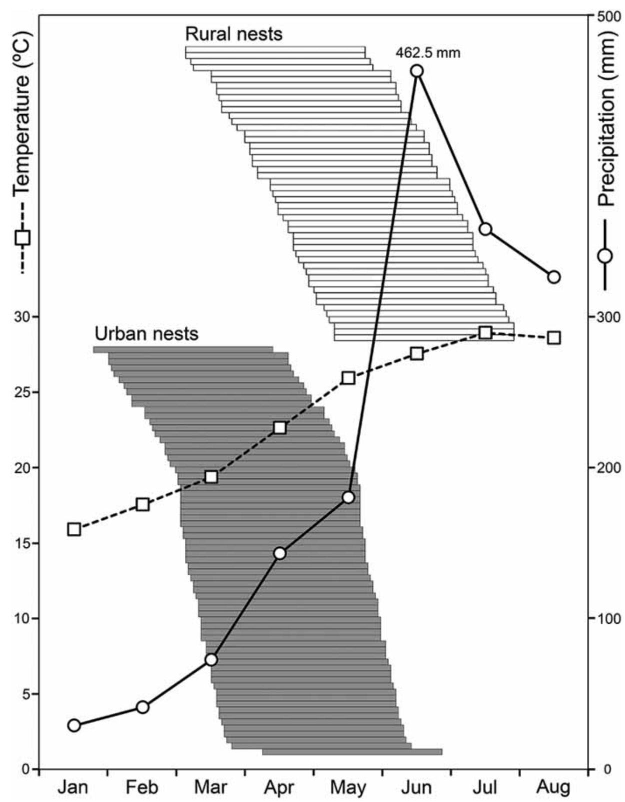

Figure 1. The egg-laying date and brooding periods of the rural Crested Goshawks (bars in white) were significantly later than their urban counterparts (bars in grey). This difference in phenology coincidently helped the urban population to avoid the heavy rainy season (the solid line).

The second prominent difference is the increase in the proportion of mixed-age pairs (a sub-adult bird coupled with adult bird) in the urban region (GLMM, habitat: $F_{1,110} = 4.1$, $P = 0.044$). The predicted probability of mixed-age pairs of urban population (30.9 ± 5.6%) was significantly higher than that of rural population (14.3 ± 5.0%) (Fig. 2). Adult males coupled with sub-adult females were more common than the reverse both in urban ($n = 17$, 81% from the total 21 cases) and rural ($n = 7$, 100%) region.

Nesting success in relation to habitats and presence of sub-adult breeders

During the incubation stage, there was no significant difference in nesting success between the two environments nor between different pairing patterns (Fig. 3a; GLMM, habitat: $F_{1,109} = 0.78$, $P = 0.38$; pairing pattern: $F_{1,109} = 1.1$, $P = 0.31$). In contrast, nesting success in brooding stage was significantly influenced by habitat with a marginal significant effect of pairing pattern (Fig. 3b; GLMM, habitat: $F_{1,95} = 10.2$, $P = 0.0019$; pairing pattern: $F_{1,95} = 3.8$, $P = 0.056$). Urban hawks had a higher success rate in the brooding stage (95.9 ± 3.3%) than rural hawks (66.5 ± 15.6%). Altogether, both breeding location and pairing pattern significantly influenced total nesting success in the final GLMM model without the effects of the interaction and Julian date (GLMM, habitat: $F_{1,107} = 4.4$, $P = 0.039$; pairing pattern: $F_{1,107} = 4.5$, $P = 0.036$; habitat*pairing pattern: $F_{1,107} = 0.08$, $P = 0.78$; Julian date: $F_{1,107} = 0.06$, $P = 0.81$). The predicted probability of total nesting success was higher in urban (89.4 ± 8.4%) than in rural (60.4 ± 20.2%) region, and was also higher in adult pairs (87.5 ± 8.4%) than in mixed-age pairs (64.6 ± 19.8%) (Fig. 3c).

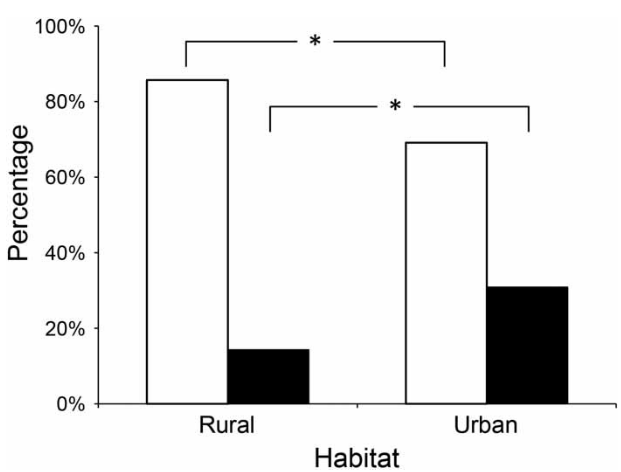

Figure 2. Urban environments had a greater proportion of mixed-age pairs (black bars) relative to adult pairs (white bars) compared to the rural environment.
*Significant difference ($P < 0.05$).

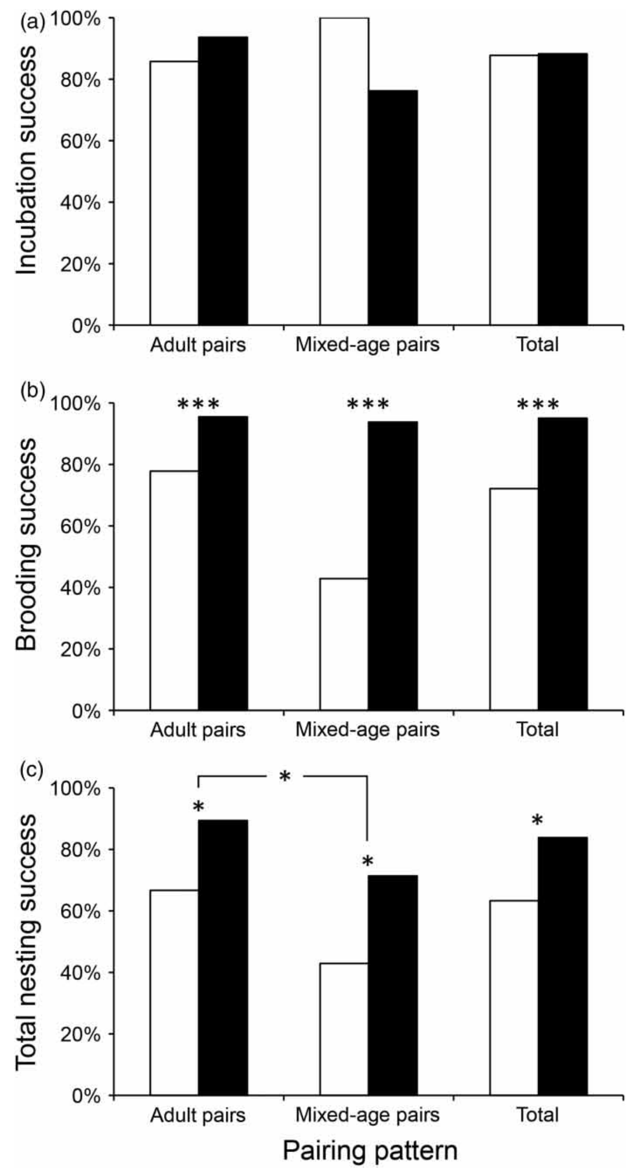

Figure 3. A comparison of incubation success (a), brooding success (b), and total nesting success (c) between different habitats (rural: white; urban: black) and different pairing pattern. (a) There was no significant difference in incubation success between different habitats and between different pairing patterns (GLMM, habitat. (b) In contrast, brooding success was higher in the urban population than in the rural population with a marginal effect of pairing pattern. (c) Total nesting success was higher in the urban population than in the rural population, and was higher in adult pairs than that in mixed-age pairs in both habitats.
*Significant difference ($P < 0.05$).
***Significant difference ($P < 0.001$).

Productivity in relation to habitats and presence of sub-adult breeders

There was no predictor variables, including breeding location, pairing pattern and Julian date, which significantly influenced clutch size (GLMM, habitat: $F_{1,108} = 0.36$, $P = 0.55$, pairing pattern: $F_{1,108} = 3.2$, $P = 0.076$, Julian date: $F_{1,108} = 0.72$, $P = 0.40$) or nestling per nest (GLMM, habitat: $F_{1,108} = 0.09$, $P = 0.76$, pairing type: $F_{1,108} = 3.2$, $P = 0.076$, Julian date: $F_{1,108} = 0.31$, $P = 0.58$). Therefore, these two traits were similar in urban and rural regions. A similar result was obtained from the analysis of fledgling numbers (GLMM, habitat: $F_{1,108} = 3.4$, $P = 0.070$, pairing pattern: $F_{1,108} = 3.1$, $P = 0.081$, Julian date: $F_{1,108} = 1.1$, $P = 0.29$). However, after we removed Julian date, the breeding location of the Goshawk (urban vs. rural) significantly affected the number of fledglings per nest (GLMM, habitat: $F_{1,109} = 15.3$, $P = 0.0002$, pairing type: $F_{1,109} = 3.1$, $P = 0.080$). The mean number of fledgling per nesting pair was higher in urban (1.18 ± 0.22) than in rural regions (0.78 ± 0.23) (Fig. 4).

Causes of nest failures between habitats

With respect to the 11 nest failure cases in urban areas, eight incubation failures and three brooding failures were recorded. Human unintentional disturbance (e.g. tree trimming) was the only factor that caused nest failure in urban areas during the six-year study. In contrast, predation and harassment by wildlife were the main factors which caused 55.6% ($n = 10$) of nest failures ($n = 18$) in rural areas. Among them, three and seven nesting attempts failed during incubation and brooding, respectively. One nest at the incubation stage was harassed by a group of Formosan macaques *Macaca cyclopis*. Although the macaques did not eat or remove the egg, they occupied the nesting tree for food and caused the hawks to abandon their nest. Two nests with eggs (totalling 4 eggs) and seven nests with nestlings (a total of 11 nestlings) were preyed on by the Taiwan beauty snake *Elaphe taeniura friesei* ($n = 6$) and Taiwan stink snake *Elaphe carinata* ($n = 3$). Five nests (27.8% in proportion) with 6 nestlings failed because of bad weather. One nest was incubated for over two months, beyond the mean of the time taken for hatching (35 days, Lin *et al.* 2008), and ultimately failed to hatch. Two nests failed during incubation for unknown reasons.

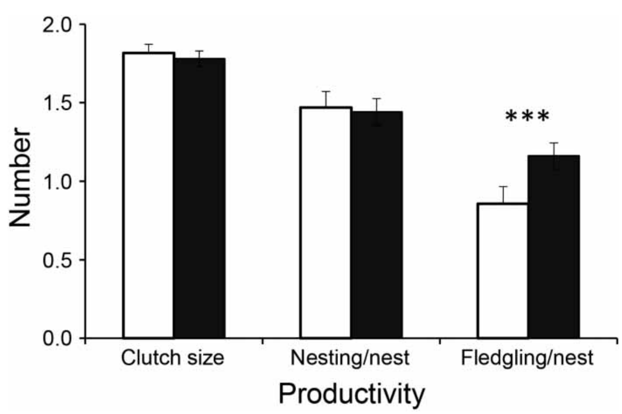

Figure 4. A comparison of clutch size, number of nestlings, and number of fledglings per nest in rural (white) and urban (black) Crested Goshawks. There was no difference in clutch size or in number of nestlings per nest but urban nests had more fledglings than rural nests.
***Significant difference ($P < 0.001$).

DISCUSSION

In some other cases, raptors established within urban areas have shown a better breeding performance than their rural counterparts, having higher nesting success, higher young production, and lower predation risk (Botelho & Arrowood 1996, Parker 1996, Rosenfield *et al.* 1996, Tella *et al.* 1996, Millsap & Bear 2000). Our results showed that lower predation risk might be one of the most critical factors that benefit urban Crested Goshawks in Taiwan. Predation was responsible for 56% of overall nesting failures in the rural environment, but this never occurred in urban areas. In rural areas, snakes were the major predator threatening eggs and early nestlings. In contrast, tree trimming by gardeners from the municipal government was the main and the only factor that caused nesting failure in urban areas.

Accurate timing of reproduction is under strong natural selection because there is often only a short period of suitable conditions for breeding in the annual cycle (Murton & Westwood 1977). On average, Crested Goshawks in the urban region bred more than one month (34 days) earlier than their rural counterparts (Fig. 1). Some other birds, including raptors (e.g. Cooper's Hawk and Tawny Owl), also show earlier reproduction in urban environments (Boal & Mannan 1999, Solonen 2014). A probable explanation for such a timing shift might relate to year-round high and stable food abundance in urban areas (Solonen & af Ursin 2008, Lepczyk & Warren 2012, Kumar *et al.* 2014). From a previous study, Crested Goshawks in urban areas take advantage of the high abundance of Tree Sparrow *Passer montanus* and Red Turtle Dove *Streptopelia tranquebarica* and prey mainly on these two species (Lin *et al.* 2008). In contrast, food abundance in the rural environment might be more seasonally limited. In some other studies, early breeding of urbanized birds may avoid interspecific resource or nest site competition (Forsman *et al.* 2002, Martin *et al.* 2014), or increase the opportunity of a second brood if the first nest fails (Newton 1979). However, we did not have a chance to test these alternative hypotheses in the current study.

Earlier breeding of Crested Goshawks in urban areas might also lead to avoidance of the rainy season (Fig. 1). Heavy rain was the second most important factor contributing to nest failures, responsible for 28% of overall nesting failures in rural areas. Average precipitation in June and July was 462.5 and 357.7 mm, respectively during the six years (2006–11), forming 35% of annual precipitation in Taichung (2054 mm annually on average, based on data from the Central Weather Bureau of Taiwan, http://www.cwb.gov.tw/eng/index.htm). The incubation and brooding of the Crested Goshawk lasts approximately 70 days; while June and July are the major period when the fledglings are vulnerable (Fig. 1). Continuous rain can be fatal to nestlings directly (e.g. hypothermia) or indirectly (e.g. starvation and parasite infection) (Calder & Booser 1973, Rogers 1987, Howe 1992, Brown & Brown 2002, McDonald *et al.* 2004), and hence increases the chance of nest failure (Kostrzewa & Kostrzewa 1990). Many long-term studies of raptors have concluded that rainfall is a major factor causing breeding failures (Kostrzewa & Kostrzewa 1990, Penteriani 1997, García & Arroyo 2001, Rodríguez & Bustamante 2003). According to our observations, parental foraging was curtailed or ceased during heavy rainfall, and so this may have resulted in a decrease in food supply. Compared to the rural hawks, most urban hawks fledged approximately one month earlier in May, just before the rainy season and coincidently avoided the impact of the heavy rains. In most cases, mature pairs are thought to have higher productivity than that of immature pairs or mixed-age pairs (Bradley *et al.* 1995, Pärt 2001, Reid *et al.* 2003). Age-assorted pairs, especially older ones, are more common in natural environments with a better nesting success (Pärt 2001). In this study, the significantly lower ratio of mixed-aged pairs in the rural habitat (Fig. 2) hinted that this kind of pairing was not favoured in this environment. Indeed, the breeding success of adult pairs was better than mixed-age pairs in both rural and urban regions (Fig. 3c). However, the nesting success of mixed-age pairs in urban areas (71.4%) was compatible to that of adult pairs in rural areas (66.7%). Possible explanations to explain the higher proportion of mixed-age pairs in urban areas, include: (1) higher mortality of adults may result in shortage of mates, which increased the chance of mixed-age pairings in urban areas (Balbontín *et al.* 2003, Whitfield *et al.* 2004); and (2) the urban areas provide high food supply and plenty of nesting sites compared to rural areas, and so more vacancies for immature birds (Newton 1992, Tordoff & Redig 1997). Although we do not have evidence to reject the first explanation, it is perhaps less probable because the hawk is still increasing in population size in the urban environment. Prey abundance is critical for birds of prey to maintain populations (Kumar *et al.* 2014), and Crested Goshawks in urban areas obviously benefit from the extra abundance of sparrows and doves (Lin *et al.* 2008).

We conclude that the urban Crested Goshawk population benefits from high food supply and low predation risk. The year-round abundance of prey might increase the breeding success of young adults, which increases the proportion of mixed-age pairs. This phenomenon may also facilitate the hawks advancing their breeding schedule, which then avoid brooding during the heavy rainy season. A combination of these factors may explain the gradual increase of the Crested Goshawks in cities: continuous monitoring of their population dynamics as these areas reach carrying capacity will be worthwhile.

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