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WINTER IRRUPTION OF TWO *GERANOAETUS* HAWKS IN THE MONTE DESERT OF ARGENTINA

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ABSTRACT.—Winter irruption refers to an unpredictable increase in the number of individuals usually dominated by one age class, either juvenile or adult, into a given area as a response to fluctuations in the food supply. Irruptions are well documented for avian predators breeding in the Arctic and Subarctic regions whereby individuals irrupt into irregular nonbreeding areas across the Boreal Temperate Region. However, this phenomenon is largely unknown across the Austral Temperate Region. We studied the age class composition of Variable Hawks (*Geranoaetus polyosoma*) and Black-chested Buzzard-Eagles (*G. melanoleucus*) during six austral winters (nonbreeding season) at an overlapping breeding and overwintering area in the Monte Desert (semiarid grassland and shrub steppes) of the Andean foothills at Mendoza province in central Argentina (33°S). We measured the overall abundance per winter (combining the five age classes) and calculated the relative abundance per age class for each winter of both species. We used the ratio of total number of individuals observed in a single winter/the total hours of observation per winter as an index of abundance, because sampling effort was not equal across winters. We found that (1) both species exhibited winter irruptions, (2) the irruptions were largely driven by a marked increase of Basic I individuals (the youngest age class); at the same time, Basic V individuals (the oldest age class) exhibited their (modestly) lowest abundance, and (3) winter irruptions might be species-specific, as the responses differed between the two species, with a joint irruption event in the austral winter 2016 and a second irruptive event only recorded for Black-chested Buzzard-Eagles in the austral winter of 2018. We posit that the marked increase of Basic I individuals during the irruptive winters cannot be fully explained by successful breeding of the local population, and is likely largely a result of individuals born elsewhere, presumably at southern latitudes, and overwintering at our study site in central Argentina.

KEY WORDS: *Variable Hawk*; Geranoaetus polyosoma; *Black-chested Buzzard-Eagle*; Geranoaetus melanoleucus; *age classes*; *nonbreeding season*; *semiarid grassland*; *shrub steppes*; *South America*.

IRRUPCIÓN INVERNAL DE DOS ESPECIES DE *GERANOAETUS* EN EL DESIERTO DEL MONTE DE ARGENTINA

RESUMEN.—La irrupción invernal se refiere a un aumento impredecible en el número de individuos generalmente dominados por una clase de edad, ya sea juvenil o adulto, en un área determinada como respuesta a las fluctuaciones en el suministro de alimentos. Las irrupciones están bien documentadas en las aves depredadoras que se reproducen en las regiones árticas y subárticas, donde los individuos irrumpen en

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áreas irregulares no reproductivas de la Región Templada Boreal. Sin embargo, este fenómeno es en gran parte desconocido en la Región Templada Austral. Estudiamos la composición por clases de edad de *Geranoaetus polyosoma* y *G. melanoleucus* durante seis inviernos australes (temporada no reproductiva) en un área de reproducción e invernada ubicada en el Desierto del Monte (pastizales semiáridos y estepas arbustivas) en las estribaciones andinas de la provincia de Mendoza, en el centro de Argentina (33°S). Medimos la abundancia general por invierno (combinando las cinco clases de edad) y calculamos la abundancia relativa por clase de edad de ambas especies para cada invierno. Usamos la proporción del número total de individuos observados en un solo invierno sobre el total de horas de observación por invierno como un índice de abundancia, porque el esfuerzo de muestreo no fue igual en todos los inviernos. Encontramos que (1) ambas especies exhibieron irrupciones invernales, (2) las irrupciones fueron impulsadas en gran medida por un marcado aumento de individuos de tipo Básico I (la clase de edad más joven); al mismo tiempo, los individuos de tipo Básico V (la clase de mayor edad) exhibieron su modestamente menor abundancia, y (3) las irrupciones invernales podrían ser específicas de cada especie, ya que las respuestas difirieron entre las dos especies, con un evento de irrupción conjunto en el invierno austral de 2016 y un segundo evento de irrupción sólo en *G. melanoleucus* en el invierno austral de 2018. Postulamos que el marcado incremento de individuos de tipo Básico I durante las irrupciones invernales no puede explicarse completamente por la reproducción exitosa de la población local, y es probable que sea en gran parte resultado de individuos nacidos en otros lugares, presumiblemente en latitudes más meridionales, que invernarían en nuestro sitio de estudio en el centro de Argentina.

[Traducción de los autores editada]

INTRODUCTION

Irruptive behavior refers to a sudden increase in the number of individuals during the breeding or nonbreeding season in a given area as a response to fluctuations in the food supply (Newton 2006, 2008). Irruptions generally involve the movement of an unpredictable yet often large number of individuals into a specific area, and occur in highly mobile species such as seed-eaters, diurnal and nocturnal raptors, and waterfowl specialized on fluctuating pulsed resources (Newton 2008, Kingsford et al. 2010, Areta et al. 2013, Pavey et al. 2020). For avian predators, the irruptive behavior can occur during the breeding or the nonbreeding seasons. Breeding season irruptions have been widely documented across the Arctic and Subarctic regions (Newton 2006, 2008) and in the desert region of Australia (Pavey et al. 2008, 2020). In contrast, nonbreeding season irruptions (hereafter winter irruptions) have only been recorded in predators specialized on fluctuating rodent populations in the Arctic and Subarctic regions; winter irruptions are likely related to the amount of food available per capita on the breeding grounds and, to some extent, the timing of the decline in prey populations (Nero and Copland 1997, Cheveau et al. 2004, Newton 2008, Graves et al. 2012, Curk et al. 2018, Santonja et al. 2019).

Two main hypotheses ("breeding success" and "lack of food") have been proposed to explain winter irruptions in avian predators across the Boreal Temperate Region (Koenig and Knops 2001, Newton 2006). Both hypotheses focus on irruptive individuals that appear in irregular nonbreeding areas, but they differ in their predictions regarding age class composition of the irruptive group (Koenig and Knops 2001, Newton 2006). The breeding-success hypothesis states that following a very successful breeding season, a higher than usual number of individuals leaving their breeding grounds will venture into an irregular nonbreeding range; thus a large proportion of the population would be composed of juveniles (Newton 2006, Robillard et al. 2016, Santonja et al. 2019). In contrast, the lack-of-food hypothesis states that post-breeding individuals would be forced to leave their regular breeding ranges (or even their regular nonbreeding ranges) due to the reduced prey availability in search of alternate areas where food is more abundant; hence a large proportion of individuals would be adults because the lack of food would have reduced their reproductive output during the breeding season (Koenig and Knops 2001, Cheveau et al. 2004, Newton 2006). These two relatively simple hypotheses appear to work well for Arctic and Subarctic irruptive predators; however, they might not be equally suited to explain winter irruptions of austral Neotropical avian predators that have partly overlapping breeding and overwintering areas and which also display delayed plumage maturation, as is the case of some avian raptors in the Southern Cone of South America such as Variable Hawk (*Geranoaetus polyosoma*), Black-chested Buzzard-Eagle (*G. melanoleucus*), and White-tailed

Hawk (*G. albicaudatus*; Cabot and de Vries 2004, Seipke 2007, Clark and Schmitt 2017, M. A. Juhant unpubl. data).

In the Austral Temperate Region of South America, the winter irruption of avian predators is almost unknown. However, this may be more a reflection of the lack of systematic and long-term surveys (Juhant 2011) than a true indication of its rarity. The Variable Hawk and Black-chested Buzzard-Eagle are two common avian predators endemic to South America. Both species breed across the Austral Temperate Region (23–55°S) and are likely partial migrants belonging to the Austral-Neotropical system (Ferguson-Lees and Christie 2001, Juhant 2011), which is composed of species that breed in the Southern Cone of South America and overwinter within temperate latitudes and/or at the tropical belt (Jahn et al. 2004). However, little is known about their migratory behavior and wintering ranges (see Capllonch and Ortiz 2009, López et al. 2017). Both species represent good candidates to study potential winter irruptions, given their mobility and specialized diet on fluctuating mammalian prey species (Jaksic et al. 1997, López et al. 2017). These species display delayed plumage maturation with five distinct age classes (Seipke 2007, M. A. Juhant unpubl. data; but see Cabot and de Vries [2004] for a different perspective), and they tend to congregate in open areas during the austral winter (nonbreeding season) across both the breeding and wintering ranges (Capllonch and Ortiz 2009, López et al. 2017, M. A. Juhant unpubl. data). This set of shared life-history traits (partial migration, five age classes, and winter aggregations) opens a bewildering range of possible scenarios of age class compositions in winter irruptions of these two species.

Here we assess the overall abundance and the relative abundance per age class in Variable Hawks and Black-chested Buzzard-Eagles during six austral winters in the Monte Desert (semiarid grassland and shrub steppes) in the Andean foothills of Mendoza province in central Argentina (33°S). We specifically asked two questions: (1) can Variable Hawks and Black-chested Buzzard-Eagles be irruptive during winter, and (2) if they do irrupt in winter, how different is the age class composition during irruptive and non-irruptive years?

Both species have a continuous distribution across the Argentine Andes (Ferguson-Lees and Christie 2001, Pearman and Areta 2020); however, precise knowledge of their spatiotemporal distribution during the annual cycle is lacking. During the austral winter, residents and overwintering individuals thought to come from farther south occur at our study site. Therefore, we also conducted a systematic road survey in 2018 across the Monte Desert encompassing a large area (25–36°S and 66–69°W) to assess the seasonal shift of abundance (austral summer vs. winter) in both species in a given year.

METHODS

Study Site. The abundance of Variable Hawks and Black-chested Buzzard-Eagles was measured annually during the austral winter in the Monte Desert (semiarid grassland and shrub steppes). The Monte Desert is located entirely within Argentina covering a latitudinal gradient of 2000 km across the Andean foothills and is mainly divided into two regions: the northern Monte dominated by mountains and closed basins (24–32°S, 66–68°W) and the southern Monte with plains and plateaus (32–44°S, 62–69°W; Roig et al. 2009). The annual rainfall ranges from <100 to 450 mm (Abraham et al. 2009); however, unusually high rainfall is typically recorded in El Niño Southern Oscillation years from October to March (Compagnucci et al. 2002). The study site is located on private land (*estancia* Lucia I. Bombal) at the foot of the *Cordón del Plata* mountain range in La Carrera (33°12.4375′S, 69°15.9277′W), Mendoza province, at an altitude of 1550–2100 masl (Supplemental Material Fig. S1). The vegetation consists of upland grassland (*Festuca* sp.), cultivated fields of alfalfa (*Medicago sativa*), potato (*Solanum tuberosum*), exotic forests (e.g., *Populus* sp.), and isolated shrubby patches. Moreover, part of the study area is used for grazing cattle and red deer (*Cervus elaphus*).

Foot Surveys. Between 15 July and 15 August during six austral winters (2011, 2014–2016, 2018, and 2019), MAJ surveyed the study area (24 km^2) on foot for a total of 66 d (11 ± 3.5 [SD] d/yr), 432 hr (72 ± 24 [SD] hr/yr), and 1244 km (207 ± 63 [SD] km/yr). The fieldwork was conducted in the middle of the austral winter when no migratory movements of any raptors are known across the Austral Temperate Region; thus, individual raptors detected during the fieldwork could safely be considered as overwintering in the study area. Field observations were conducted between 0830 and 1830 H (GMT-3) using semi-structured walks covering the entire study area at an average walk-speed of 3.0 ± 0.4 (SD) km/hr. A starting point was established at the center of the study area and used across seasons to conduct the semi-structured walks leading in different directions. Each walk was performed twice, forward and backward with excellent visibility to detect individual raptors. Frequent stops to scan the field using a pair of Swarovski 10 × 50 binoculars were made to aid in the detection of individual raptors. Every detected individual was photographed either perching or flying (most of the time both) at a range of up to 300 m, identified using individual-specific field marks, and assigned to one of five age classes, which were validated afterward by assessing in detail the photographs obtained. Photographs of each individual were labeled and stored in individual folders and sorted by age class, creating a permanent archive; folders include photos of individuals that might be photographed more than once in the same austral winter but not across austral winter years (see below for further details).

Camera Equipment. The camera equipment included a Panasonic Lumix DMC-FZ50 with a Panasonic 1.7X Teleconverter (2011), Canon EOS 7D with a Canon EF 400 mm f/5.6L (2014–2016 and 2018), and a Canon EOS 7D Mark II with a Canon EF 400 mm f/5.6L (2019).

Individual Identification Based on the Appearance of Flight Feathers and Color Traits. Individual-specific field marks allowed reliable individual identification, preventing double-counting of the same individual within each austral winter. Both species are highly variable in their non-definitive and definitive plumages, and individual-specific field marks included variation of feathers molted among the flight feathers (primaries, secondaries, and rectrices), distinctive patterns of broken (usually older feathers) and worn flight feathers (see age class assignment for further details), and color variation of the breast, belly, upper and under wing coverts, upper and under tail coverts, and tail. The combination of these individual-specific traits was used to avoid double counting the same individual within each austral winter; however, it was not possible to identify individuals across winters because individual-specific traits during one season were not present during subsequent seasons.

Age Class Assignment Based on Molt of Flight Feathers, Especially Primaries. Age class nomenclature follows Howell et al. (2003), and is based on the annual molt cycles of the flight feathers (primaries, secondaries, and rectrices). Across the Austral Temperate Region both species molt between mid-spring and early autumn (M. A. Juhant unpubl. data); therefore, individuals generally reach the austral winter with the most advanced plumage they were able to afford energetically, and this is particularly true for birds in non-definitive plumages. In Accipitriformes, the molt pattern in primaries is the most accurate way to assign individuals to a given age class, because a new molt wave is initiated at primary 1 at the start of every annual molt cycle, regardless of whether all primaries were replaced or not in the previous cycle (Clark 2004). Following this criterion, individuals of both species can be assigned to one of five age classes: Basic I individuals (approximately 7–8 mo old or first winter) show a single generation of primary feathers and no molt waves. Basic II individuals (approximately 19–20 mo or second winter) show two generations of primaries and one molt wave. Basic III individuals (approximately 31–32 mo or third winter) show three generations and two molt waves. Basic IV individuals (approximately 43–44 mo or fourth winter) show two generations and three molt waves. Finally, Basic V individuals ($\geq$ 55–56 mo or $\geq$ fifth winter) have acquired the definitive basic (adult) plumage and replaced all primaries at least once; at this point, it is no longer possible to precisely age individuals by assessing their molt in the flight feathers. New and old flight feathers can be distinguished reliably by their wear and color pattern (older feathers are lighter and more abraded than newer ones) and shape (the flight feathers of individuals in Basic I plumage are shorter, narrower, and more pointed at the tip than those of the more advanced age classes, resulting in a ragged trailing edge to the wing that is noticeable in flight).

Assessment of Winter Irruptions and Seasonal Abundance in the Monte Desert. We defined a winter irruption as an event in which an unusual increase in the number of individuals was recorded in a given austral winter and this high abundance was clearly marked by an increase of one of the extreme age classes, either Basic I (juvenile) or Basic V (adult; Newton 2006). We used the ratio of total number of individuals observed in a single winter/the total hours of observation per winter as an index of abundance, because sampling effort was not equal across winters. The total number of individuals excludes resightings in a given austral winter, which was possible because individual birds were identified using individual-specific field marks. For each austral winter, we calculated the overall abundance per winter (combining the five age classes) and the relative abundance per age class. We compared the overall abundance and the relative abundance per age class (assessed separately for Basic I and Basic V, and Basic II, III, and IV) among austral winters to assess the occurrence of irruptive events based on (1) a great increase in overall abundance and (2) an increase in numbers in one of the extreme age classes, either Basic I or Basic V. Additionally, we calculated the ratio of the relative abundance of the extreme age classes. Once an irruptive event was assigned, we performed descriptive statistics to assess the differences in the overall abundance, the relative abundance of age classes, and the ratio of the extreme age classes by dividing the value of the irruptive event with the non-irruptive events. We report the mean, standard deviation, and ranges for all results.

Road Surveys in 2018. To assess whether a seasonal shift of abundance occurred during a given year across the Monte Desert, a systematic road survey was carried out by MAJ and an assistant (the driver) in March (late-austral summer) and in June (early-austral winter) of 2018 (see Supplemental Material Fig. S1). The survey covered a total distance of 1950 km (3900 km in both seasons combined) in 11 d (22 d both seasons combined) at a vehicle speed of 30–50 km/hr. The survey encompassed a large latitudinal gradient of 1135 km (25–36°S) and a smaller longitudinal gradient (66–69°W) across Salta, Tucumán, Catamarca, La Rioja, San Juan, Mendoza, and La Pampa provinces (see Supplemental Material Appendix S1 for detailed road-survey protocol and description and Fig. S1). We used the absolute number of individuals recorded and calculated the number of individuals per 50 km to determine the cumulative frequency per species for each season.

RESULTS

Winter Irruptions in the Monte Desert. During the six austral winters (2011, 2014–2016, 2018, 2019) a total of 678 individuals were recorded (252 Variable Hawks and 426 Black-chested Buzzard-Eagles). The absolute number of individuals per age class exhibited yearly fluctuations in both species (Table 1).

Variable Hawks exhibited one winter irruption event during the austral winter 2016, with a 3.65-fold (± 0.70; 2.64–4.40) increase in the overall abundance compared to the other five austral winters (Fig. 1A). During the irruptive winter, the relative abundance of the youngest age class, Basic I, increased 6.97 fold (± 2.84; 3.17–9.95); the oldest age class, Basic V, decreased 0.33 fold (± 0.13; 0.21–0.50; Fig. 1B). The ratio Basic I:Basic V in the

Table 1. Number of individuals of Variable Hawks (*Geranoaetus polyosoma*) and Black-chested Buzzard-Eagles (*G. melanoleucus*) recorded during six austral winters (nonbreeding season) at an overlapping breeding and overwintering area in the Monte Desert (semiarid grassland and shrub steppes) of the Andean foothills at Mendoza province in central Argentina (33°S). Numbers in parentheses represent total number of individuals observed in a single winter/the total hours of observation per winter. Two irruptive events, one in 2016 in both species and another in 2018 only in Black-chested Buzzard-Eagles, were detected by an overall increase in the absolute number of birds and their relative abundance, largely driven by a marked increase of Basic I (juveniles) individuals. Survey effort for each austral winter was as follows (2011: 52 hr, 180 km); (2014: 70 hr, 198 km); (2015: 66 hr, 196 km); (2016: 95 hr, 212 km); (2018: 106 hr, 324 km); (2019: 43 hr, 134 km).

AGE CLASS	NO. OF VARIABLE HAWKS						NO. OF BLACK-CHESTED BUZZARD-EAGLES					
	2011	2014	2015	2016	2018	2019	2011	2014	2015	2016	2018	2019
Basic I	4 (0.08)	2 (0.03)	2 (0.03)	76 (0.80)	0 (0.00)	1 (0.02)	2 (0.04)	11 (0.16)	14 (0.21)	51 (0.54)	41 (0.39)	3 (0.07)
Basic II	2 (0.04)	5 (0.07)	11 (0.17)	14 (0.15)	10 (0.09)	0 (0.00)	8 (0.15)	10 (0.14)	16 (0.24)	42 (0.44)	40 (0.38)	5 (0.12)
Basic III	5 (0.10)	5 (0.07)	8 (0.12)	18 (0.19)	16 (0.15)	2 (0.05)	12 (0.23)	3 (0.04)	10 (0.15)	19 (0.20)	30 (0.28)	5 (0.12)
Basic IV	0 (0.00)	5 (0.07)	0 (0.00)	4 (0.04)	2 (0.02)	3 (0.07)	5 (0.10)	3 (0.04)	5 (0.08)	8 (0.08)	9 (0.08)	4 (0.09)
Basic V	10 (0.19)	6 (0.09)	12 (0.18)	14 (0.15)	8 (0.08)	7 (0.16)	15 (0.29)	11 (0.16)	13 (0.20)	10 (0.11)	13 (0.12)	8 (0.19)
Total	**21 (0.41)**	**23 (0.33)**	**33 (0.50)**	**126 (1.33)**	**36 (0.34)**	**13 (0.30)**	**42 (0.81)**	**38 (0.55)**	**58 (0.88)**	**130 (1.37)**	**133 (1.25)**	**25 (0.58)**

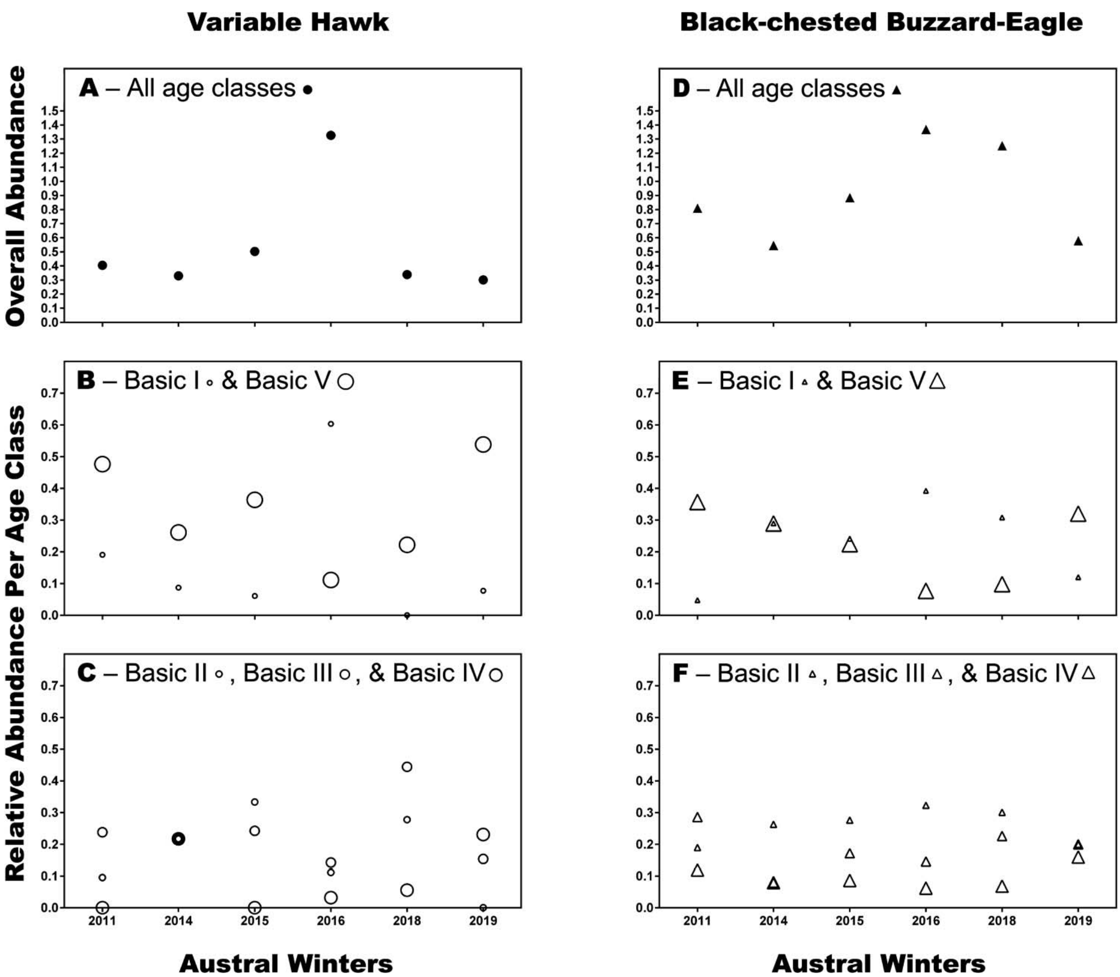

Figure 1. Overall abundance per winter (total number of individuals observed in a single winter/the total hours of observation per winter) of the five age classes combined (A, D) and the relative abundance per age class for each winter (B–C, E–F) in Variable Hawks (*Geranoaetus polyosoma*) and Black-chested Buzzard-Eagles (*G. melanoleucus*), respectively, recorded during six austral winters (nonbreeding season) at an overlapping breeding and overwintering area in the Monte Desert (semiarid grassland and shrub steppes) of the Andean foothills at Mendoza province in central Argentina (33°S). Irruptive events occurred in 2016 for both species and in 2018 for Black-chested Buzzard-Eagles only. All irruptions showed an increase in overall abundance caused by a marked increase of the relative abundance of Basic I (juveniles) individuals and an inverted ratio of Basic I (juveniles):Basic V (adults) in comparison to non-irruptive years.

irruptive winter was 5.43, a reversed pattern of abundance as compared to that of non-irruptive winters, in which that ratio was 0.26 (± 0.13; 0.14–0.40), excluding the extreme 2018 winter when no Basic I individuals were recorded (Table 1, Fig. 1B). The relative abundance of the three remaining age classes, Basic II, III, and IV, fluctuated but did not show any clear pattern of change between the irruptive and non-irruptive winters (Fig. 1C).

Black-chested Buzzard-Eagles exhibited two winter irruption events during the austral winters 2016 and 2018 with a 2.03-fold (± 0.48; 1.55–2.51) and 1.86-fold (± 0.44; 1.42–2.30), respectively, increase in overall abundance compared to the other four austral winters (Fig. 1D). During the irruptive winters, the relative abundance of the youngest age class, Basic I, increased 3.62 fold (± 3.19; 1.36–8.24) and 2.85 fold (± 2.51; 1.06–6.47); and the oldest age class, Basic V, decreased 0.27 fold (± 0.06; 0.22–0.34) and 0.34 fold (± 0.07; 0.27–0.44), respectively (Fig. 1E). The ratios Basic I:Basic V in the irruptive winters were 5.10 and 3.15, a reversed pattern in comparison to the non-irruptive winters, in which that ratio was 0.65 (± 0.46; 0.13–1.08; Fig. 1E). The relative abundance of the three remaining age classes, Basic II, III, and IV, fluctuated but did not show any clear pattern of change between the irruptive and non-irruptive winters (Fig. 1F).

Seasonal Abundance in the Monte Desert. Variable Hawks outnumbered Black-chested Buzzard-Eagles in both seasons across the seven Argentine provinces. A total of 59 individual Variable Hawks were recorded in March and 97 individuals in June, a cumulative frequency (frequency sum of the number of individual per 50 km) of 1.18 individuals in March and 1.94 in June (a 1.64-fold increase in the austral winter). A total of 11 individual Black-chested Buzzard-Eagles were recorded in March and 55 individuals in June, a cumulative frequency of 0.22 individuals in March and 1.10 in June (a 5.00-fold increase in the austral winter). For further details on the seasonal abundance of both species as determined by the road survey, see Supplemental Material Appendix A-1.

Discussion

Winter Irruptions and Age Class Composition in the Monte Desert. Here we have shown that Variable Hawks and Black-chested Buzzard-Eagles can exhibit winter irruptions, as evidenced by sharp increases in the overall abundance of the two species during the austral winter 2016, and only Black-chested Buzzard-Eagles during the austral winter 2018. The pronounced increase in overall abundance was mostly due to the marked increase in Basic I individuals, whereas Basic V individuals exhibited their (modestly) lowest relative abundance during the irruptive winters. We suspect that the Basic I individuals recorded might have come from elsewhere (presumably from southern latitudes), because if the Basic I individuals had been hatched in the study area and surrounding areas, the Basic V individuals (breeding class) would not have shown the lowest relative abundance during the winter irruptions but instead would have had high numbers. Interestingly, during the austral winter 2016, when both species were irruptive at our study site, an unusual congregation of Black-chested Buzzard-Eagles (mostly individuals in non-definitive plumage) was reported at a similar semiarid grassland in central Argentina, 550 km southeast of the study site (López et al. 2017). Collectively, these observations suggest that a wide-scale winter irruption took place during 2016 in central Argentina.

Several factors, such as the degree of diet specialization (e.g., high vs. low), type of prey consumed, flexibility in habitat use, breeding strategy (e.g., average clutch size), mobility, and body size have been proposed to influence the response of irruptive migrants to resource fluctuations (Cheveau et al. 2004, Yamaguchi et al. 2017). Because their responses differed, the causes of winter irruptions of Variable Hawks and Black-chested Buzzard-Eagles might be species specific. The size difference between Variable Hawks (500–1280 g; Dunning 2008) and Black-chested Buzzard-Eagles (1670–3200 g; Dunning 2008) and likely diet specialization might result in different species-specific responses to fluctuations in food resources. The species seemed to capture different prey items at our study area and elsewhere. In Mendoza, Variable Hawks were seen feeding on small mice and yellow-toothed cavies (*Galea musteloides*), while Black-chested Buzzard-Eagles took yellow-toothed cavies and European hares (*Lepus europaeus*). The winter diet of Variable Hawks in the Pampas consisted mostly of small rodents (*Akodon azarae*, *Calomys* spp. and *Ctenomys talarum*) (Baladrón et al. 2006, 2009) and the winter aggregation of Black-chested Buzzard-Eagles in semiarid grassland in central Argentina was thought to be linked to a population explosion of yellow-toothed cavies (López et al. 2017). Moreover, the abundance of European hare influences the abundance of Black-chested Buzzard-Eagles during the breeding season (Barbar et al. 2018). These differences in feeding habits may explain why in the austral winter 2018 Variable Hawks showed a low overall abundance with no Basic I recorded, whereas Black-chested Buzzard-Eagles showed the second highest peak in both overall abundance and relative abundance of Basic I.

We were unable to find any clear pattern of change in the three remaining age classes, Basic II, III, and IV (individuals in non-definitive plumage) in relation to irruptive winters and non-irruptive winters. Although the abundance of these age classes fluctuated over the six austral winters, their dynamics may depend on multiple factors that are difficult to assess and require further research.

The fieldwork was time-restricted and did not allow us to follow how irruptions developed. As this study was conducted in the middle of the austral winter, we are confident that we did not miss other irruption events across the winter surveys, as it is highly unlikely that such an event would occur later in the season. However, more protracted sampling across the austral summer (breeding season) and winter (nonbreeding season) are necessary to further elucidate the duration and intensity of irruptions.

Seasonal Abundance in the Monte Desert. In the Austral Temperate Region, the detailed spatiotemporal distribution of Variable Hawks and Black-chested Buzzard-Eagles is largely unknown. Our seasonal abundance surveys indicate a seasonal shift in the abundance of both species across the Monte Desert, with a clear increase of individuals during the austral winter. However, we must stress that the road survey conducted in 2018 coincided with the second irruptive event of the Black-chested Buzzard-Eagle in our study area, and thus the marked increase in abundance during winter may not be representative of typical winter abundance in the region.

The Monte Desert serves as overlapping breeding and overwintering (during the austral winter) areas due to the great latitudinal gradient it encompasses along the Andean foothills (22–44°S) and its open areas of semiarid grasslands and shrub steppes, which constitute the main habitats of both species (Ferguson-Lees and Christie 2001). Long-term large-scale quantitative studies during the austral summer and winter across the Monte Desert are needed to better understand the fluctuations in abundance of the different age classes of Variable Hawks and Black-chested Buzzard-Eagles and their relationship to prey density and environmental conditions.

Winter Irruptions and Delayed Plumage Maturation. Studying irruptive behavior is challenging because it requires long-term monitoring of abundance, as well as the skills to properly assign individuals to the correct age class, especially in species that exhibit delayed plumage maturation. Additional predictions are needed to better understand winter irruptions in species that exhibit delayed plumage maturation, because the two main currently accepted hypotheses—breeding-success and lack-of-food (Koenig and Knops 2001)—offer predictions only for the extreme age classes (juvenile and adult). Making clear predictions relating to the intermediate age classes is more difficult given that their life history traits are less well known. Species such as the Rough-legged Hawk (*Buteo lagopus*), in which individuals irrupt into irregular nonbreeding areas across the Boreal Temperate Region (Bosakowski and Smith 1992, Britt 2009) and have four distinguishable age classes (Clark and Bloom 2005), as well as the Variable Hawk and Black-chested Buzzard-Eagle (each with five distinguishable age classes), can be important in the search for and development of new hypotheses. Testing these hypotheses depends critically on correctly assigning age classes during irruptions. For example, the bulk of individuals of Black-chested Buzzard-Eagles recorded during the winter irruption of 2016 by López et al. (2017) were reported as juveniles, immatures, and subadults (instead of referring to them as Basic I to Basic IV), making it difficult to correctly interpret the age class composition of this event. In this context, learning how the migratory behavior develops between the juvenile and adult stages will provide insightful information on the nature of winter irruptions and help to develop new predictions for intermediate age classes.

Conclusions. This study represents the first empirical comparison of overall abundance and age class fluctuations in Variable Hawks and Black-chested Buzzard-Eagles over several austral winters at an overlapping breeding and overwintering site in the Monte Desert of Argentina. We posit that the marked increase of Basic I individuals during the irruptive winters cannot be fully explained by successful breeding of the local populations, and is likely largely a results of individuals born elsewhere, presumably at southern latitudes, and overwintering at our study site in central Argentina.

SUPPLEMENTAL MATERIAL (available online). Appendix S1: Road-survey protocol and description. Figure S1: Geographic distribution of study sites and transects where seasonality and abundance of Variable Hawk (*Geranoaetus polyosoma*) and Black-chested Buzzard Eagle (*G. melanoleucus*) were assessed during this study.

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