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Ornithology

Web-sourced photographic methods reveal dietary composition and shifts in resident and migrant *Coracias* rollers in southern Africa

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Abstract

Closely related species coexisting in the same niche often have dietary overlap and interspecific competition can result in resource partitioning e.g., dietary shifts, migration or phenological changes. Traditional methods to study avian diets are typically costly, difficult, and invasive. Using web-sourced photographs is an emerging, non-invasive method to study avian foraging ecology. We used this approach, along with photographic road surveys, to study prey composition of migratory European Rollers *Coracias garrulus* and resident Lilac-breasted Rollers *Coracias caudatus* where they co-occur in southern Africa. These insectivorous sister species are frequently photographed with prey in their bills because of their conspicuous perch-and-wait foraging behaviour and bright plumage coloration. We collated over 250 photographs of rollers holding prey and identified prey items representing 15 animal orders. Lilac-breasted Roller diet contained six unique orders of prey during the Austral summer (when the European Roller is present), and only one during winter (when the European Roller has migrated north). This suggests that Lilac-breasted Rollers may broaden their diet seasonally to alleviate competition with European Rollers during summer. Additionally, Lilac-breasted and European Rollers had an 84% overlap in dietary composition, potentially representing high interspecific competition - even during wet savanna summers when resource abundance is high - that might have originally driven the evolution of migratory behaviour in the European Roller. Our findings expand the current knowledge of roller diets and highlighting the growing role of social media in ecological studies.

Introduction

The family Coraciidae, commonly known as rollers, consists of two genera, *Coracias* and *Eurystomus*, and twelve species (Johansson et al. 2018). These species are distributed throughout Africa, Europe, southern Asia and Australia and are named for their acrobatic displays in flight (Clarke et al. 2009). *Coracias* is distinguished by their robust, straight bill with a small hook rather than a short, broad bill in *Eurystomus* (Johansson et al. 2018). Rollers in the *Coracias* genus often perch and wait for prey, while *Eurystomus* hawk insects in the air (Johansson et al. 2018). Such is the case for a sister species pair of *Coracias* rollers that co-occur in southern Africa in the austral summer: the European Roller *C. garrulus* and the Lilac-breasted Roller *C. caudatus* (Johansson et al. 2018).

The European Roller is a non-breeding summer migrant to sub-Saharan African (Hockey et al. 2005; Figure 1). Their breeding range extends from southern and central Europe into northern Africa, and east into Siberia and Iran (Hockey et al. 2005). The Lilac-breasted Roller is non-migratory (resident) and endemic to Africa, widely distributed south of the Sahara Desert (Hockey et al. 2005; Figure 2). The ranges of these two species overlap in summer (from November to March) in southern Africa (Hockey et. al. 2005).

Migratory behaviour appears to be uniquely derived (autapomorphic) in European Rollers, as the Coraciidae originated in Africa and the European Roller is the only *Coracias* species to breed in Europe (Fry & Fry 1992). This is in line with a global pattern where the primary drivers of migratory behaviour in birds appear to be of recent origin and due to resource abundance and geographic isolation, not shared ancestry (Piersma et al. 2005, Dingle 2008).

When two species have identical niches, one will outcompete the other for resources and ultimately supplant them. The concept of limiting similarity proposes the existence of a maximum level of niche overlap between two given species that will allow continued coexistence (MacArthur & Levins 1967). We speculate that migration likely arose in European Rollers in response to prey availability: they breed in their northern range during the boreal summer (Fry & Fry 1992) and arrive in southern Africa at the beginning of the wet austral summer when insects are abundant (Ogilvie 2007). The European Roller is more commonly seen in southern Africa during wet years (Kemper 2015). These migration patterns suggest that the European Rollers migrate to exploit abundant food sources, as Lilac-breasted Rollers outcompete them for prey resources when they are both present in southern Africa.

Diets influenced by resource partitioning

According to the competitive exclusion principle, where two species occupy the same niche, natural selection will favour a shift to partition resources (Gause 1932). This is to avoid interspecific competition for food or habitat requirements that can potentially reduce fitness, allowing coexistence and preventing extinction (Schoener 1974, Martin 1996). Lilac-breasted and European Rollers are expected to partition resources to decrease competition because they share similar niches when European Rollers are present in southern Africa. However, little has been done to investigate resource partitioning, and whether this would be achieved through dietary or habitat preference shifts.

European Rollers breed in Europe and migrate to Africa in November, staying until March (sometimes May; Hockey et al. 2005; Figure 1A), coinciding with the wet summer season when an abundance of insects emerges after winter (Ogilvie 2007). For our study, European Rollers were assumed to be present in southern Africa if observations were recorded between November and April. The diet of European Rollers includes locusts, beetles, grasshoppers, crickets, ants, termites, wasps, bees, and some small vertebrates (Hockey et al. 2005, Cassola & Lovari 1979, Kiss 2014, Catry et al. 2019).

Lilac-breasted Rollers are resident and endemic to Africa (Figure 1B) and breed during the Austral summer (September until January). They are temporarily territorial for feeding habitats, often evenly spaced, especially when density is high during the breeding season (Hockey et al. 2005). The high competition for preferred open feeding habitats during this period may have implications for thermal physiology, such as thermoregulation and evaporative heat loss. Their diet includes scorpions, spiders, solifugae, centipedes, caterpillars, grasshoppers, crickets, mantids, beetles, moths, butterflies, ants, and termites (Hockey et al. 2005, Kopji et al. 2000). They also consume small rodents and reptiles such as snakes, lizards, shrews, and mice and often eat noxious prey species with chemical defenses (Hockey et al. 2005).

Lilac-breasted and European Rollers have similar habitat preferences: they prefer savannas or open woodland areas with perches for foraging and both species are attracted to dry areas with frequent bushfires as they stir up insects for an easy meal (Fry & Fry 1992, Hockey et al. 2005). Both species employ a “sit and wait” technique, perching on dead branches, poles, or bushes near roads (Hockey et al. 2005).

One of the mechanisms which facilitates the coexistence of species with similar ecological niches is spatial niche partitioning (Pickett et al. 2018, Roeleke et al. 2018). This has been documented in two open-space foraging bats, which shift their space use in response to competition with one another with one species exploiting more distant foraging spaces (Roeleke et al. 2018). However, instead of shifting habitat preferences to coexist, we predict that the Lilac-breasted Roller likely changes dietary preferences to avoid competition. The European Roller possibly influences the diet of the resident Lilac-breasted Roller as the two species have extremely similar diets and foraging behavior (Hockey et al. 2005).

Mixed methodological approaches for studying avian diets

Traditional approaches for studying bird diets are often costly, difficult, and invasive, e.g., induced regurgitations, stomach flushing, and dissections (Gaglio et al. 2017). Early research on European Roller diets sampled food remains (pellets) from nests during the breeding season (Cassola & Lovari 1979). Similarly, stomach contents have been dissected out of Lilac-breasted Rollers to identify ingested prey items (Kopji et al. 2000; Appendix 1). Other studies have determined prey availability for European Rollers using pitfall traps to catch invertebrates near nests (Kiss 2014) and removing regurgitated pellets from nests (Catry et al. 2019; Appendix 2). These methods, though effective, disrupt the natural behaviour of rollers, where photography-based methods allow researchers to observe rollers foraging without disturbing their natural activity patterns.

Photography and video recordings of European Rollers delivering prey to nests have been used to complement invasive research techniques (Kiss 2014) to study chick provisioning. Rollers often perch holding prey in their mouths before ingesting it, making them ideal for photography-based diets studies (Hockey et al. 2005). Photography based diet surveys reduce disturbance to the birds, but effort and cost remain high. Sourcing photographs from web-based platforms to study avian diets has proven cost effective and a viable alternative to traditional techniques (Gaglio et al. 2017, Leighton et al. 2016, Panter & Amar 2021).

Web-sourced photography is an emerging tool that allows for comprehensive sampling at minimal costs that has been used to explore diets of other bird species such as the Martial Eagle *Polemaetus bellicosus* and the Eurasian Sparrowhawk *Accipiter nisus* (Naude et al. 2019, Panter & Amar 2021). These studies collected photographs from online platforms e.g., Google images, citizen science websites, and social media using automated and manual searches that generated data on diet composition of these birds without requiring physical field work. Our study aims to test if similar techniques can be used to study the foraging ecology of European and Lilac-breasted Rollers.

Our study aims to explore the dietary overlap between the Lilac-breasted Roller and European Roller when both species are present in southern Africa. We predict there will be some overlap in the prey species consumed by these closely related species because of their similar feeding behaviours. We expect competition-induced dietary shifts in Lilac-breasted Rollers when European Rollers arrive in southern Africa in the austral summer: we hypothesize that when European Rollers are present, Lilac-breasted Rollers will broaden their dietary niche, consuming a wider variety of prey i.e. resource partitioning to avoid foraging competition with the migratory European Roller.

Methods and Materials

Road surveys

Our fieldwork was conducted in southern Kruger National Park (KNP), Mpumalanga, South Africa. This area is associated with the highest numbers of observations of European and Lilac-breasted Rollers in southern Africa based on citizen science through the South African Bird Atlas Projects (SABAP1 and SABAP2) ((Underhill 2016, Underhill et al. 2017, Lee et al. 2022) (Figure 2). Our study area extended from the Crocodile River — the Park's southern boundary to the Sabie River flowing from Skukuza to Lower Sabie (Fourie 1992). Geologically the park has two almost equal sections: granite in the west and basalts in the east divided by a narrow belt of sandstone and shale in the centre (Fourie 1992). Our study area covers both sediment types (Figure 3).

Kruger National Park can be divided into eight major vegetation types: sandveld, mopaneveld, savanna grasslands, mixed broadleaf woodlands, thorn thicket, foothills, and riverine bush (Fourie 1992). These broad vegetation types can be divided further into fine scale landscape types. We sampled a wide variety of tar and gravel roads

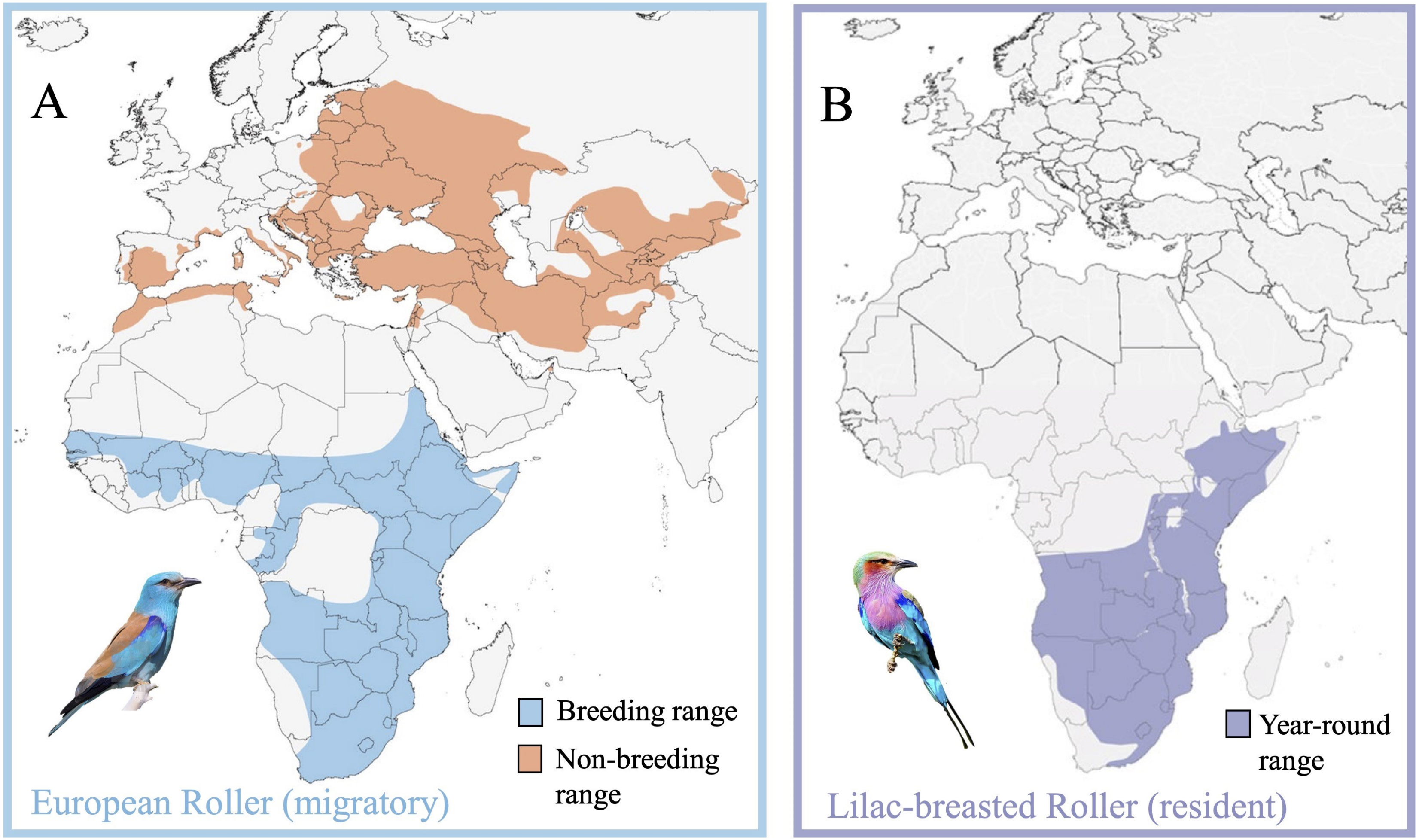

Figure 1: Distribution of (A) the migratory European Roller across its breeding (Boreal summer) and non-breeding (Austral summer) ranges and (B) the resident Lilac-breasted Roller Coracias caudatus (from Handbook to the Birds of the World Alive).

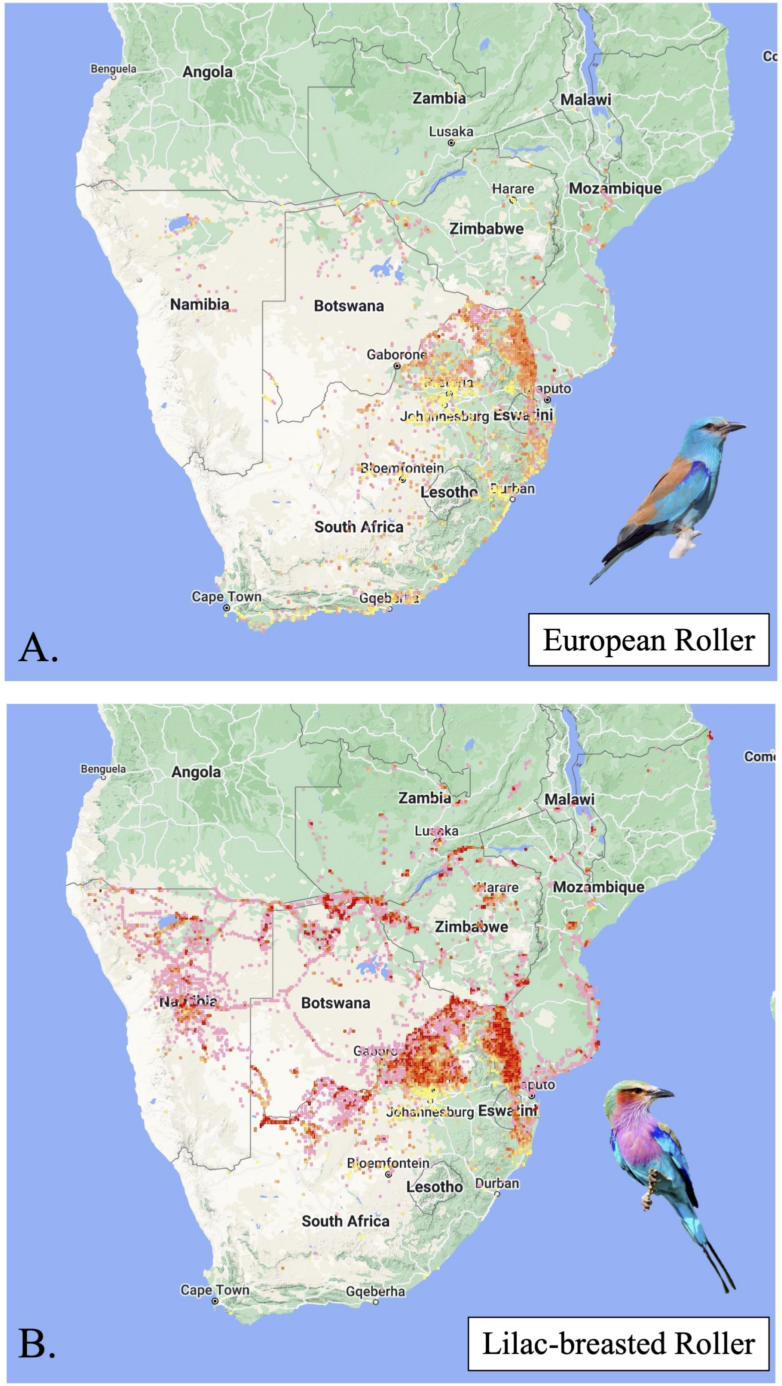

Figure 2: Second South African Bird Atlas Project (SABAP2) observation records for (A) the European Roller and (B) the Lilac-breasted Roller. Warmer colours indicate a larger reporting rate, i.e. that a larger proportion of the checklists for the grid cell have the species recorded.

across multiple vegetation types (Figures 3 & 4). The main vegetation types sampled were bushwillow rugged veld, marula tree savanna, mixed bushwillow savanna, and euphorbia mountain bushveld. We observed Rollers across five days in late April 2022 using binoculars and cameras (Sony Cyber-Shot RX10 Mark IV and Canon EOS250D). Our data collection protocol included date, time, GPS location, and road type (Figure 5). If the roller moved during the allotted time (Figure 6), we continued to monitor it while it was within view. We observed each roller for a maximum of 15 minutes, regardless of the number of prey captures. We took photographs for prey identification.

Global Biodiversity Information Facility (GBIF)

The Global Biodiversity Information Facility aims to provide open access data for all life on earth through an international network and data infrastructure (GBIF 2022). The database draws together data from a multitude of sources including museum specimens, occurrence records, and smartphone photos (GBIF 2022). Biodiversity data is accessible through the network of publishers applying shared principles to describe and record data (GBIF 2022).

We searched for the European and Lilac-breasted Roller by species at (https://www.gbif.org/species/search). Using GBIF advanced search generator, we investigated the diets of European and Lilac-breasted Rollers. We searched using the scientific names "*Coracias garrulus*" for European and "*Coracias caudatus*" for the Lilac-breasted Rollers. Accurate coordinates were *required* in our search settings and *media type* was set to "image". We did not specify a specific time frame and confined our search to five countries in southern Africa: Namibia, Botswana, Zimbabwe, Mozambique, and South Africa. All results from the GBIF database were research grade findings from iNaturalist and Observation.org. These are crowdsourced species identification systems for recording personal observations and collaborating with others (iNaturalist 2021, Observation.org 2022).

Instagram

Instagram is a social media network primarily for sharing photos and videos (Instagram 2022). Users can upload content to share publicly, with followers, or to specific users (Instagram 2022). Instagram uses hashtags (#) to label and categorize content (Instagram 2022) Hashtags can also be used to make posts more visible to the public (Instagram 2022). If a public account uses a hashtag, the post becomes visible on the corresponding hashtag page (Instagram 2022). Hashtags can be searched for individually on Instagram's search page.

Using a manual search on Instagram, we identified photos of European and Lilac-breasted Rollers posted before 25 April 2022. We limited our search to the 100 most recent photos of each species to obtain a large enough sample to assess their diets. We searched using #europeanroller and #lilacbreastedroller and required the photographs to have the location specified by geotag, hashtag, comment, or account name. We only included photos from the same southern African countries stipulated in our GBIF search. Sometimes more specific location data were available such as game reserves, camps and national parks within these countries. We did not include videos or any photos with #repost to avoid repeat-counting prey items. We recorded username, species, location, country, and hashtags. We also noted if the photograph was in a collage and if the collage contained multiple photos of the same feeding event. Relevant hashtags specified location or prey species.

Prey identification from photographs

We identified prey to order level (Picker et al. 2002, Scholtz & Holm 2008) and employed the suborders Lacertoidea and Serpentes instead of order Squamata to distinguish between lizards and snakes respectively. Unidentifiable images from our study, GBIF, and Instagram were noted as unknown.

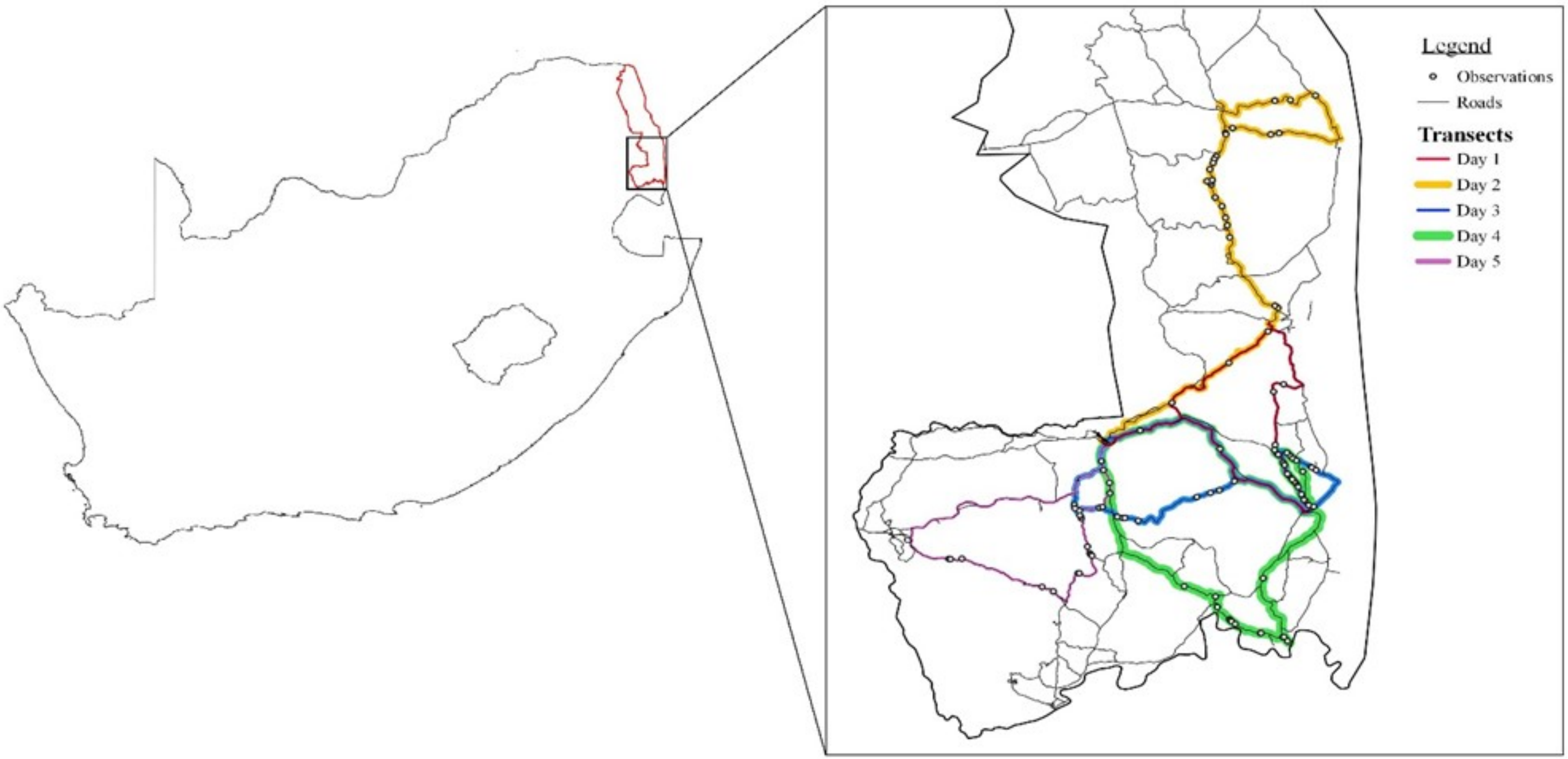

Figure 3: Transects from our experimental study in lower KNP. Our study included five transects (one per day) beginning and ending in Skukuza. Transect one (pink) was from Skukuza to Lower Sabie on H4-1 and to Tshokwane on S128 and H10, then back to Skukuza on H1-2. Transect two (yellow) was from Skukuza to Satara H1-2 and H1-3, making a loop on S90, S41, and S100 before returning on the same path. Transect three (orange), Skukuza to Pretoriuskop, was from H1-1 to S20, then to Afsaal on H2-2. We went back to Skukuza on H3, connected to S112, S22, S114, and H1-1. Transect four (green) was from Skukuza to Crocodile Bridge on H1-1, S114, S26, and S25, then to Lower Sabie on H4-2. We traveled from Lower Sabie to Skukuza on H4-1 again. Finally, transect five (blue) was from Skukuza to Lower Sabie on H1-1, S114, S21, and H4-1. We made a loop near Lower Sabie on S128 to S29 before heading back to Skukuza on H4-1 as before.

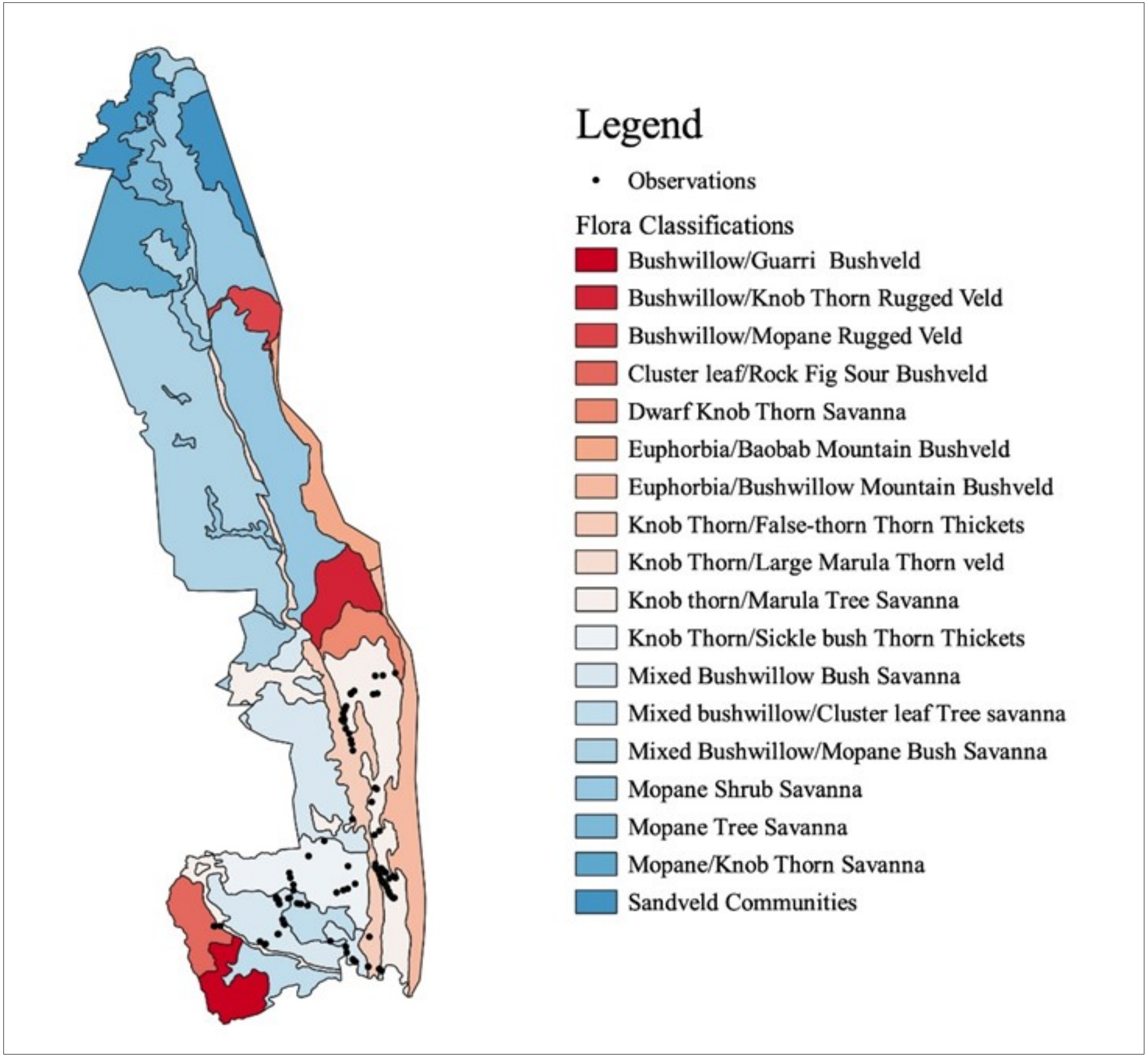

Figure 4: Map of the flora classifications for Kruger National Park, South Africa, and Lilac-breasted Roller observations from our study.

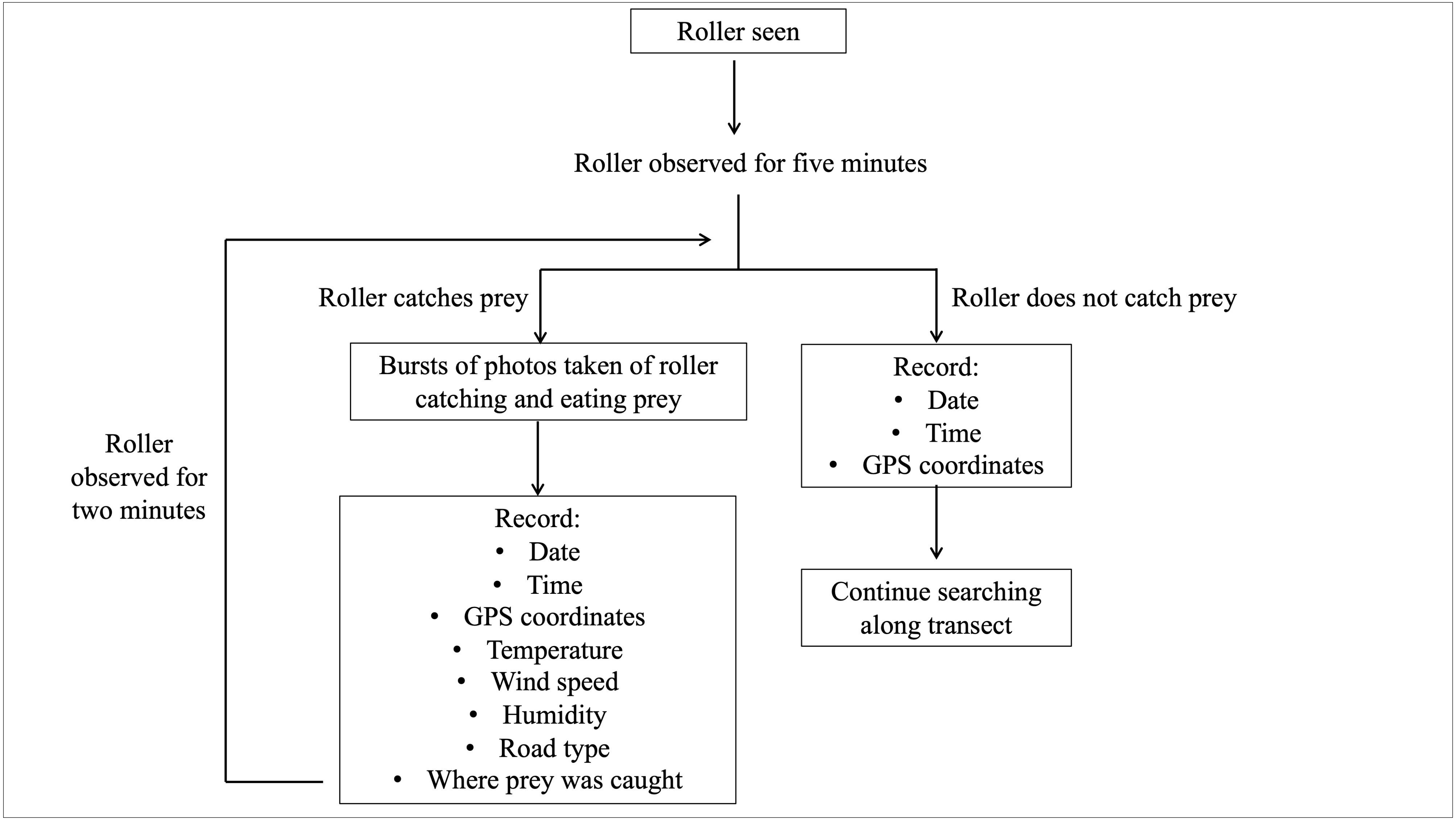

Figure 5: Flow chart outlining methods for photographing roller prey items and data collection protocols during road surveys.

Data analysis

Spatial visualisation of prey captures along transects and flora classifications were generated in QGIS 3.16.16-Hannover. To investigate the influence of roads on prey capture, data were classified by proximity to road (on or off road) substrate (tar or gravel). To compare the information available on Lilac-breasted Roller diets among three photography-based data sources, we collected, saved, and classified photographs based on prey identity. We also used Instagram data to calculate the proportions of each prey order represented in the (1) Lilac-breasted Roller diet and (2) European and Lilac-breasted Roller diet when they co-occur in southern Africa. Similarly, we use these data to quantify and visualize dietary overlap and breadth. Microsoft Excel version 16.58 was used to compile data and draw graphs to visualize the data.

Results

Positive prey identifications were made in 254 photographs of rollers holding prey. These photographs were sourced from GBIF, Instagram, and road surveys. A representative selection of these photographs is displayed in Appendix 3.

Road Surveys

We observed a total of 129 Rollers across the five transects. All birds, except two, were *Coracias caudatus* (Lilac-breasted Roller), and the others were *Coracias naevius* (Purple Roller). Of the 127 Lilac-breasted Rollers, we observed 53 actively catching or eating prey. We obtained 26 photos of the rollers eating and identified prey to the order level in all 26 photos. Of the 53 observations of rollers catching prey, 46 were of rollers catching prey from the road, rather than in or around the surrounding vegetation (Figure 6). Of these, 29 were observed on the dirt road and 17 on the tar road (Figure 6).

Global Biodiversity Information Facility (GBIF) and Instagram

Our search criteria for GBIF generated a total of 1,100 photos of Lilac-breasted Rollers and 456 European Rollers. A total of 37 of these (n = 18 Lilac-breasted and n = 19 European Rollers) had prey items in their bills. Most of the photographs were sourced from iNaturalist with only four across both species from Observation.org and photos ranged from 2009 to 2022. The 100 most recent photos from Instagram spanned from 22 April 2022 to 21 January 2018 for the European Roller and 22 April 2022 to 4 October 2020 for the Lilac-breasted Roller.

Comparing methodologies

The dietary proportions of the Lilac-breasted Roller prey showed similar patterns across sampling methodologies: our study, Instagram photos and GBIF photos (Figure 7). Grasshoppers and crickets (Orthoptera), and beetles (Coleoptera) made up the biggest proportion of diet for all three photograph sources, similar to previous invasive studies (Cassola & Lovari 1979, Kopji et al. 2000). Photos from Instagram showed the widest range of prey orders, with nine orders being represented. These results also reflected the proportions of prey orders found in previous studies of Lilac-breasted Roller stomach contents (Kopij et al. 2000; Appendix 1); except for smaller items like termites and cockroaches. Seven orders of prey were represented in our study and three orders were represented in GBIF (Figure 7).

Dietary shifts in the Lilac-breasted Roller

Differences in the diets of Lilac-breasted Rollers were detected when European Rollers were present and absent in southern Africa (Figure 8). The Lilac-breasted Roller consumed eight prey orders throughout the year and expanded the number of prey orders to 14 when the European Roller was present (Figure 9). Of the eight prey orders represented throughout the year, the proportions of Orthoptera, Anura and Scorpiones decreased when the European Roller was present (Figure 8). In contrast, there was only one additional prey order consumed by

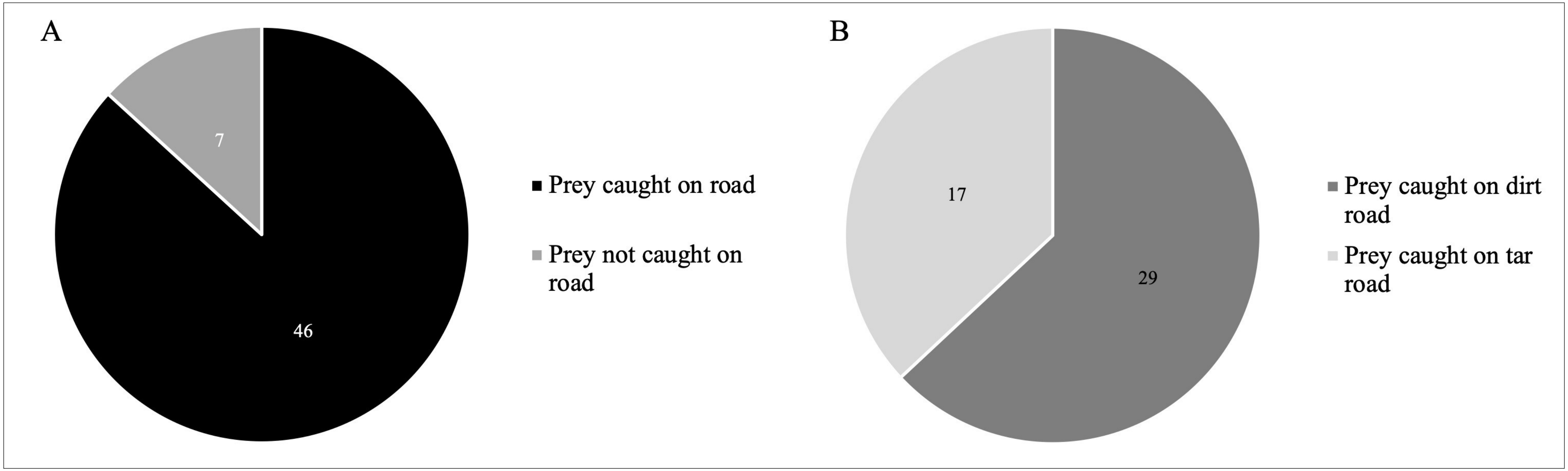

Figure 6: (a) Number of Lilac-breasted Rollers that caught prey on the road and not on the road. (b) Number of Lilac-breasted Rollers that caught their prey on the dirt road and on the tar road of the Lilac-breasted Rollers that caught prey on the road.

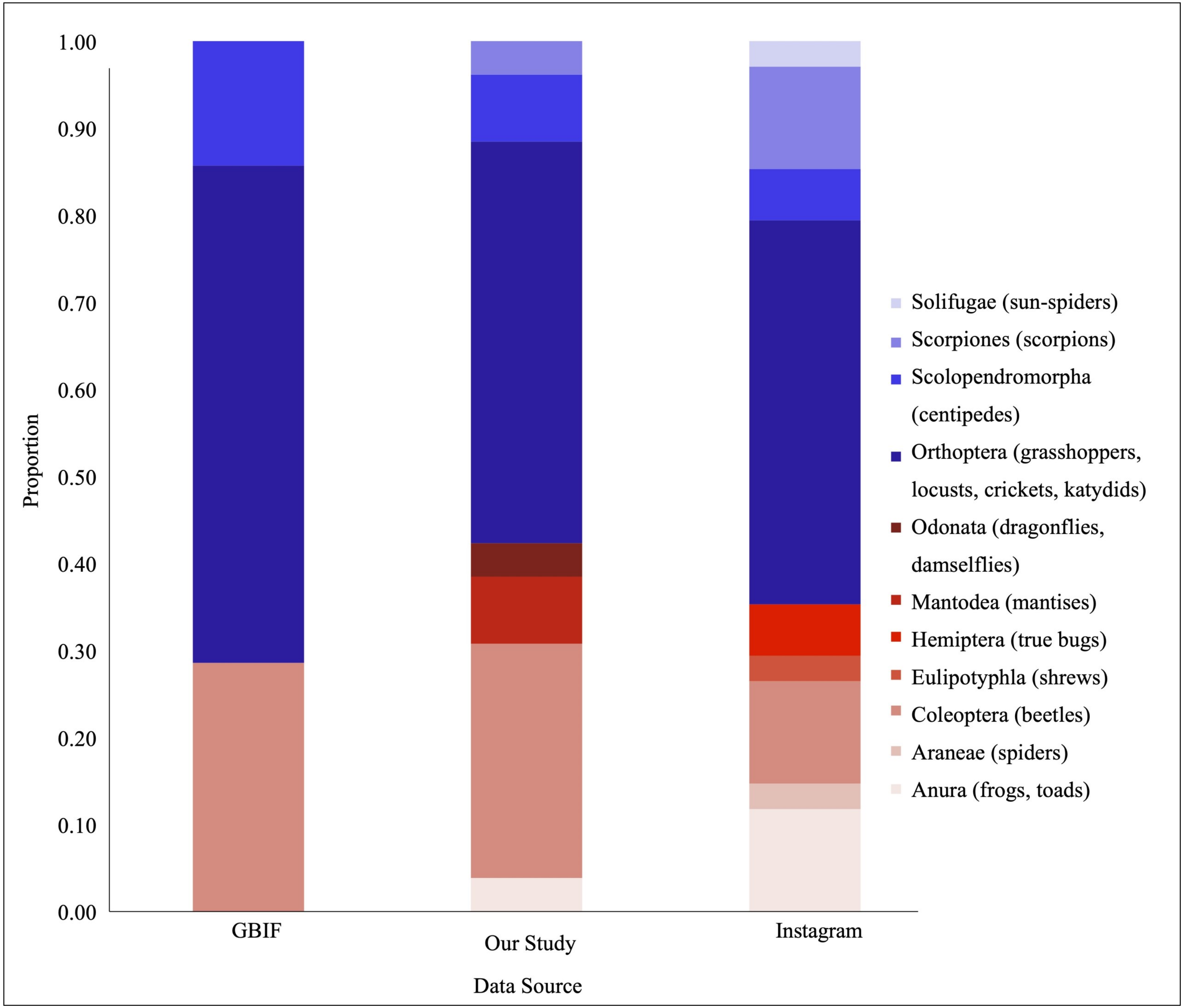

Figure 7: Proportion of prey order observed for each methodology used in this study (n = 7 photographs from GBIF; n = 26 for our study; n = 34 for Instagram) for Lilac-breasted Rollers in southern Africa when European Rollers are not present (austral winter). The number of orders represented in each methodology is given by the numbers above each bar.

the Lilac-breasted Roller when the European Roller was not present (Figure 9). When the European Roller is present, the Lilac-breasted Roller consumes 23% unique prey items. However, when the European Roller is not present, the Lilac-breasted Roller consumes only 3% unique prey items.

Dietary overlap between roller species

The diets of European and Lilac-breasted Rollers observed in Instagram photos when both species are present in southern Africa overlap for nine of the prey orders (Figure 10). The prey orders Hemiptera, Lacertoidea, Odonata, Serpente, and Spirostreptida were only identified in photos of Lilac-breasted Rollers, while Hymenoptera was only identified in European Roller photos. Both species' diets consisted mainly of Coleoptera and Orthoptera (Figure 11). Overall, 84% of all prey items consumed by the Lilac-breasted Roller were also represented in European Roller diets, while the remaining 16% appear unique to Lilac-breasted when both Roller species are present. Interestingly, 99% of all prey items consumed by the European Roller were also represented in Lilac-breasted Roller diets. Only 1% of all prey items are exclusively consumed by the European Roller when both roller species are present (Figure 11).

Discussion

In the novel field of crowd-sourced, web-based ecological research, photographic studies are emerging as an effective technique to study avian ecology (Kiss 2014, Leighton et al. 2016, Naude et al. 2019, Panter & Amar 2021). We applied these techniques, alongside photographic road surveys, to study the dietary overlap and shifts in dietary breadths of rollers in southern Africa for the first time. We found Instagram to be the most informative data source for studying the diets of European and Lilac-breasted Rollers of the platforms considered. Instagram had the highest number of prey orders represented and highest sample size compared to GBIF and the road surveys we conducted (Figure 7). Additionally, Instagram provided the highest number of photographs across shorter time spans and best represented the diversity of prey found in previous studies of stomach contents and regurgitated pellets collected from rollers (Appendices 1 & 2). We therefore used Instagram to investigate resource partitioning between the European and Lilac-breasted Rollers and dietary shifts in the Lilac-breasted Roller with changes in the presence of the European Roller in southern Africa during the Austral summer.

Using Instagram to answer ecological questions

Lilac-breasted Rollers have a taxonomically wider dietary breadth when European Rollers are present in southern Africa compared to when they have migrated north. Lilac-breasted Rollers have six unique orders of prey when the European Roller is present and only one when it is absent (Figures 10 & 11). When both species are present, European Rollers do not eat four of these six unique orders. This suggests that the Lilac-breasted Roller may shift its diet to other prey orders which are less preferred. Thus, Lilac-breasted Rollers may occupy a different dietary niche with a wider dietary breadth compared to European Rollers to avoid the potential decreases in fitness associated with interspecific competition for food (Martin 1996). This is consistent with other resident bird species which shift their diets in the presence and absence of migratory species (Chipley 1976, Waide 1981, Rabøl 1987).

Although the diets of each species have been investigated separately, the degree of dietary overlap between the species in southern Africa is unknown (Kopji et al. 2000, Catry et al. 2019). These two closely related species (Johansson et al. 2018) share similar physiology and energetic activity profiles, which result in compositional, temporal, and spatial overlap in their foraging ecology. Therefore, we expect the two species to have similar arthropod prey order preference based on digestibility and nutritional value (Reeves et al. 2021). Accordingly, we found a dietary overlap of nine prey orders. However, the number of prey orders unique to Lilac-breasted Rollers is higher than that of European Rollers (Figures 10 & 11), suggesting a higher diversity of low -frequency prey consumed by Lilac-breasted Rollers. Previous studies have shown that high frequency prey orders, such as Coleoptera and Orthoptera, have higher nutritional value than low frequency prey

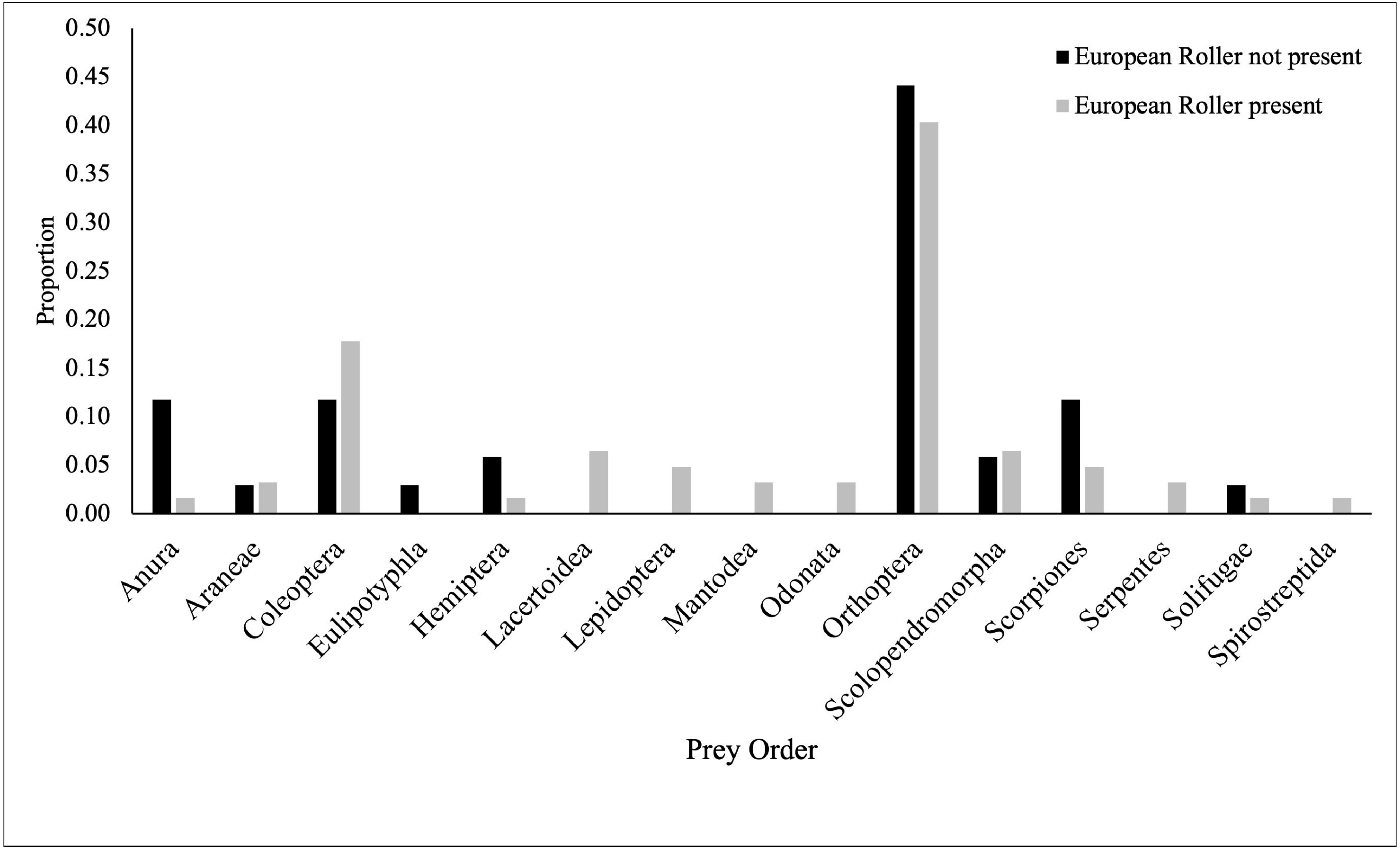

Figure 8: Proportion of the diets of Lilac-breasted Rollers in southern Africa for each prey order when the European Roller is present (from November to April) and not present (from May to October), retrieved from Instagram photos.

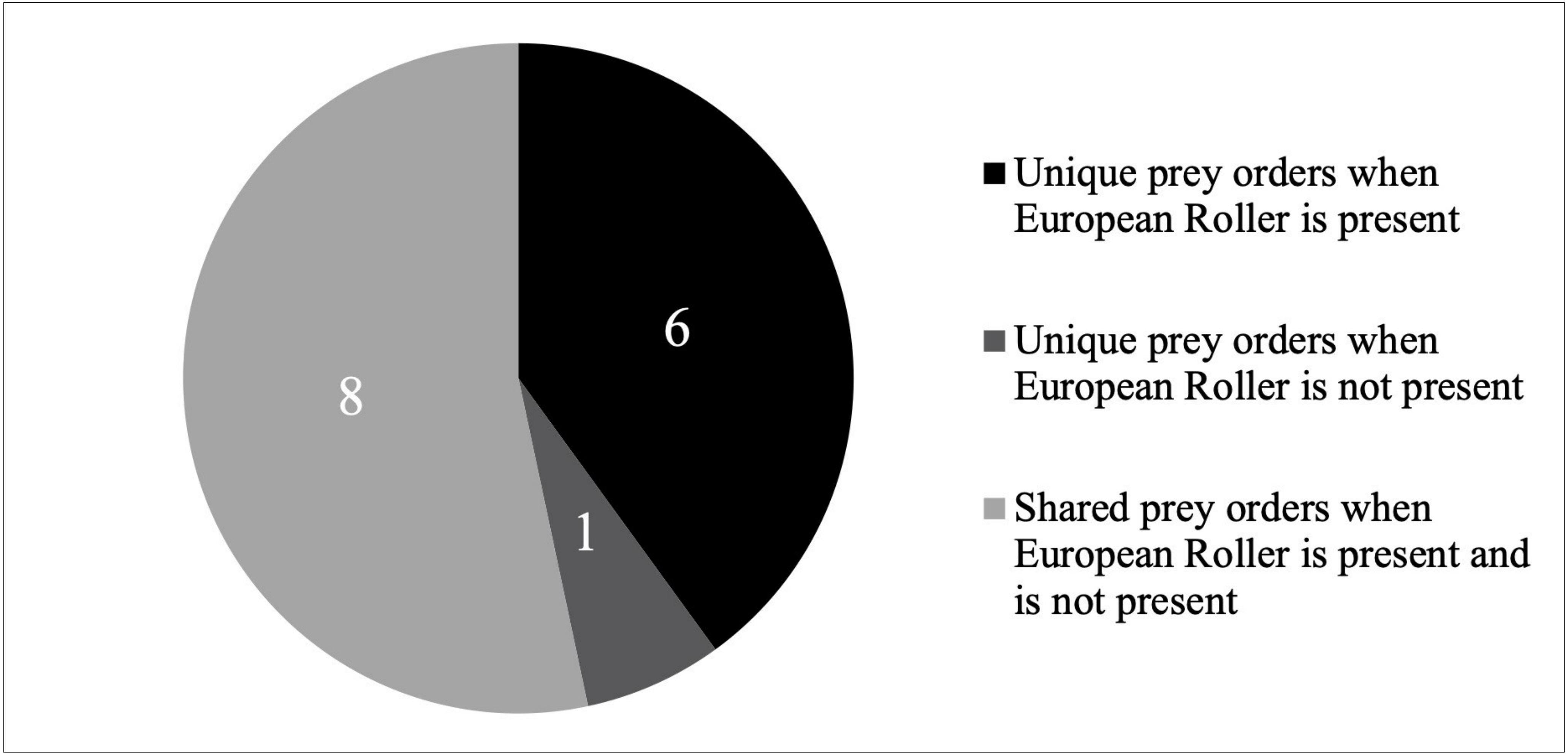

Figure 9: Number of prey orders represented in the Lilac-breasted Rollers' diet depending on the presence or absence of the European Roller.

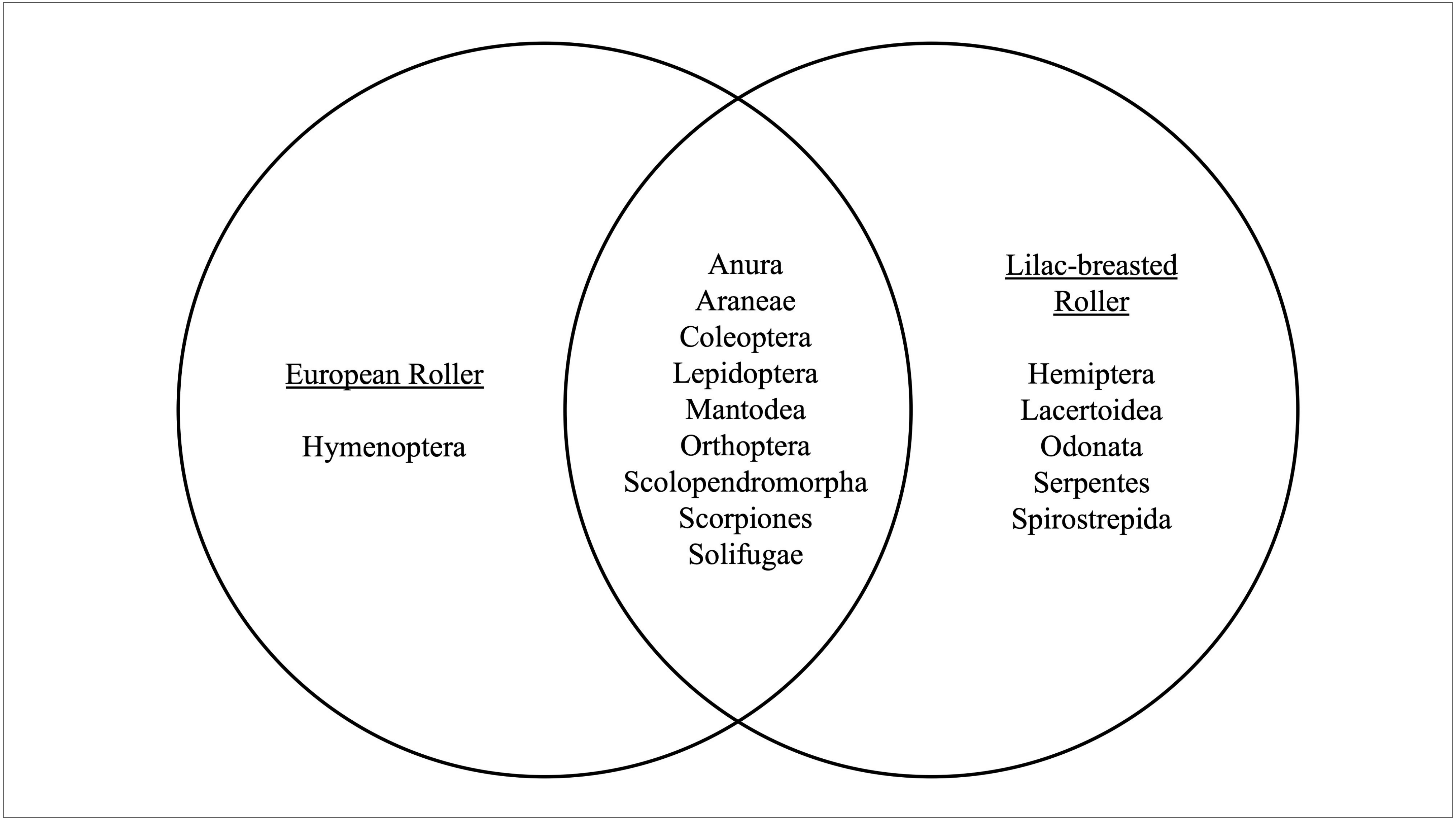

Figure 10: Venn diagram comparing the orders of prey of European and Lilac-breasted Rollers in southern Africa when the European Roller is present, retrieved from Instagram photos.

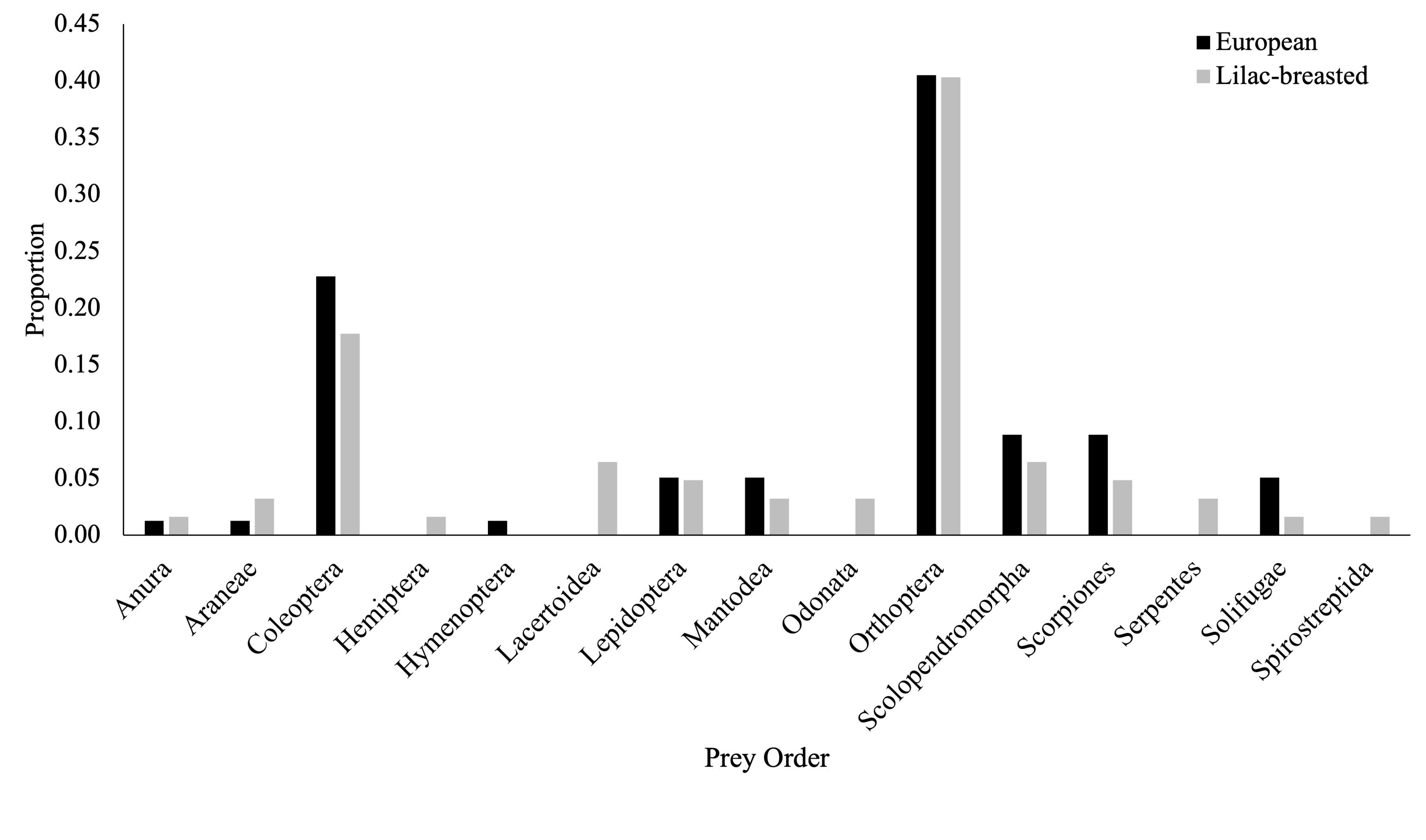

Figure 11: Proportion of European and Lilac-breasted Rollers' diets in southern Africa for each order of prey when the European Roller is present, retrieved from Instagram photos.

orders like Odonata (Razeng & Watson 2015). Thus, the presence of interspecific competition when European rollers are present may drive Lilac-breasted rollers to widen their diet to include less preferred, lower quality arthropod prey orders. These shifts have been observed in other studies which show that generalist resident species may shift to under-exploited niches to avoid competition with migrant species (Jedlicka et al. 2006). This is surprising, since migrant bird species are less specialized in their foraging habits than are resident species (Salewski 2000). This leads to many migrant species having a wider dietary breadth than resident species due to the use of opportunistic and specialized foraging techniques, respectively (Salewski et al. 2003).

Despite the Lilac-breasted Roller having a larger dietary breadth than the European Roller, their five unique prey orders only made up a small portion (16%) of their diet. Over 84% of all prey orders consumed by both the Lilac-breasted and European Roller were shared between the two species. This high dietary overlap during a period of high resource abundance suggests that interspecific competition pressure may not be high enough to cause resource partitioning for the two species (Ogilvie 2007). In the dry season when resources are scarce, competition would theoretically intensify and could have driven the evolution of migration in the European Roller.

Comparing digital photography studies with invasive studies

Many traditional dietary studies of avian species involve invasive methods (Gaglio et al. 2017). Such invasive methods have been employed to analyze the stomach contents of Lilac-breasted Rollers (n = 9; Kopij et al. 2000), detecting six prey orders from 61 items, where our photography-based study found 15 prey orders from 140 photographs of Lilac-breasted Rollers consuming prey (Appendix 1). Similarly, 11 orders of prey were identified from eight regurgitated pellets consisting of 1417 prey items for the European Roller (Catry et al. 2019), where our study found 15 prey orders from 114 photographs (Appendix 2). This shows that non-invasive digital photography methods are comparable to traditional invasive methods and may even capture a wider range of prey orders. However, unlike photographic methods, invasive techniques allow for identification of prey orders of smaller sizes such as termites (Isoptera) and flies (Diptera). However, software programs, such as Image J, can be used to estimate the size of prey in photographs. Use of these techniques may reveal differences and shifts in prey size preference between the Lilac-breasted and European Rollers.

Evaluation of photographic sources

Each photographic survey method has benefits and drawbacks. The use of digital photography to investigate potential dietary shifts and resource partitioning for Lilac-breasted and European Rollers was possible due to the foraging behaviour of these species, including the high density of these species near highly trafficked roads to catch prey (Figure 6). Although our study shows digital photography can offer insight into the diets of birds across time, it is important to consider the shortcomings of the sources of these photos before making conclusions about ecological questions like these. Photos obtained from each of the three methodologies in this study (GBIF, Instagram, and road surveys) differ in their strengths and weaknesses.

Instagram

Since photographs from Instagram had the highest photograph quality, highest sample size (n = 100), and a time period of over a year for each Roller species, this source was preferable to road transects and GBIF for answering our ecological questions. Our study assumes that European Rollers are not present in southern Africa from May to October, and present from November to April (Hockey et al. 2005). This is reflected in iNaturalist observations for European Rollers, which are proportionally low in those months (Figure 12). Unexpectedly, photos of European Rollers were posted in May, June, August and October and no photos were posted in September and December (Figure 13). This suggests that photos from Instagram may not be posted in the month in which they were taken, highlighting a potential drawback of utilizing Instagram. Our study controlled for this by excluding Instagram photos of European Rollers posted from May to October. Future studies using Instagram, and other social media platforms, should be cautious of assuming the date on which a photograph is posted as a proxy for the date on which the photograph was taken. Although the sample size was high over a time span of three years, the effort associated with sorting through photos produced by the search engine was high. This was due to manually identifying photos which matched our full search criteria, since users can only filter by one hashtag per search.

GBIF

Unlike Instagram, the sample size associated with photos extracted from GBIF was low (n = 20) despite these photos spanning a period of 13 years. However, GBIF provided the coordinates and exact dates of each observation, and had low sorting effort due to the website's filter options extracting photos which fully matched our search criteria.

Road surveys

The road surveys provided photos for only five consecutive days and the sample size is seemingly low (n = 30). However, this sample size is comparable to that of Instagram when photographs of Lilac-breasted rollers are limited to when European Rollers are absent (n = 34). Additionally, allow for the exact coordinates, dates, and times for each observation to be recorded. This method also allows for the recording of additional environmental variables, such as temperature, humidity, wind speed, road type and location of prey capture providing an opportunity to further investigate the foraging ecology of birds and how these behaviours interact under different environmental conditions.

Limitations of digital photography

Considering the vast differences in these three methodologies, we suggest that the most effective method is a combination of all three to answer ecological questions about birds. This can be guided by the strengths and weaknesses of road surveys, GBIF and Instagram (Table 1). Although photographic studies can be used to investigate the diets of birds across time, there are limitations associated with these methodologies that should be considered in the future.

Based on the evaluation of each photograph source, we suggest: (1) the Instagram search expands to include and exclude multiple hashtags and locations, (2) ecologists, as part of their work and contribution to their field, should populate citizen science databases in order to allow other researchers full transparency and access to photographs from studies, and (3) road transect studies must be run across a wider time and geographical range.

Photographic studies investigating the diets of birds are biased towards prey of larger sizes, unlike invasive techniques. This was evident during our road surveys, where Lilac-breasted Rollers were observed repeatedly foraging around termite mounds, but capturing termites as prey items was impossible due to their small size. Stomach content analyses have shown that Isoptera (termites) are a large portion (29.5%) of the Lilac-breasted Rollers' diet (Kopij et al. 2000). Photography cannot capture smaller prey such as termites, ants, and some beetles at a high enough resolution to be identified accurately. Thus, a large portion of rollers' diets may not be represented/ reflected/captured in photographic methods. This limitation is reflected in Panter & Amar (2021), which categorized photos of sparrowhawk prey by size (small, medium, and large) and found that large prey items were three times more likely to be photographed and identified, and medium sized prey were overestimated in comparison to small prey. In addition, the sole use of photographs to investigate birds' diets only allows for the identification of prey items to the order level. By not identifying prey to the species level, dietary studies may not be able to capture patterns of resource partitioning or dietary shifts over time. Further studies should investigate the diets of rollers based on the size of the prey items and composition of prey identified to the species level.

Conclusion

We have used digital photographs sourced from Instagram, road transects, and GBIF to show that Lilac-breasted Rollers have a wider dietary breadth when European Rollers are present in southern Africa compared to when they migrate north, and the two roller species have a large dietary overlap. These observations are likely attributed to re-

Table 1: Summary of the features of photographic data extracted from (i) road surveys, (ii) the Global Biodiversity Information Facility (GBIF), and (iii) Instagram methodologies used in this study.

	Road Surveys	**GBIF**	**Instagram**
Exact coordinates	Yes	Yes	No
Photography quality	Variable	Medium	High
Sample sizes per species	n = 30	n = 20	n = 100
Highest level of temporal accuracy	Time	Date	Date
Date accuracy	Exact	High	Poor
Timespan of our study	5 days	13 years	3 years
Timespan of database	N/A	13 years	12 years
Extent of spatial coverage	southern Kruger National Park	southern Africa	southern Africa
Control over spatial coverage	High	Low	Low
Certainty of bird ID based on search criteria	N/A	High	Low–Medium
Sorting effort after search criteria is applied	N/A	Low	High
Estimated time spent extracting photos	55 hours	2 hours	5 hours
Additional environmental variables associated with photograph collection	Temperature, humidity, wind speed, road type, location of prey capture	None	None
Costs and equipment associated with photograph collection	Petrol, camera, car, computer	Computer	Computer, social media account

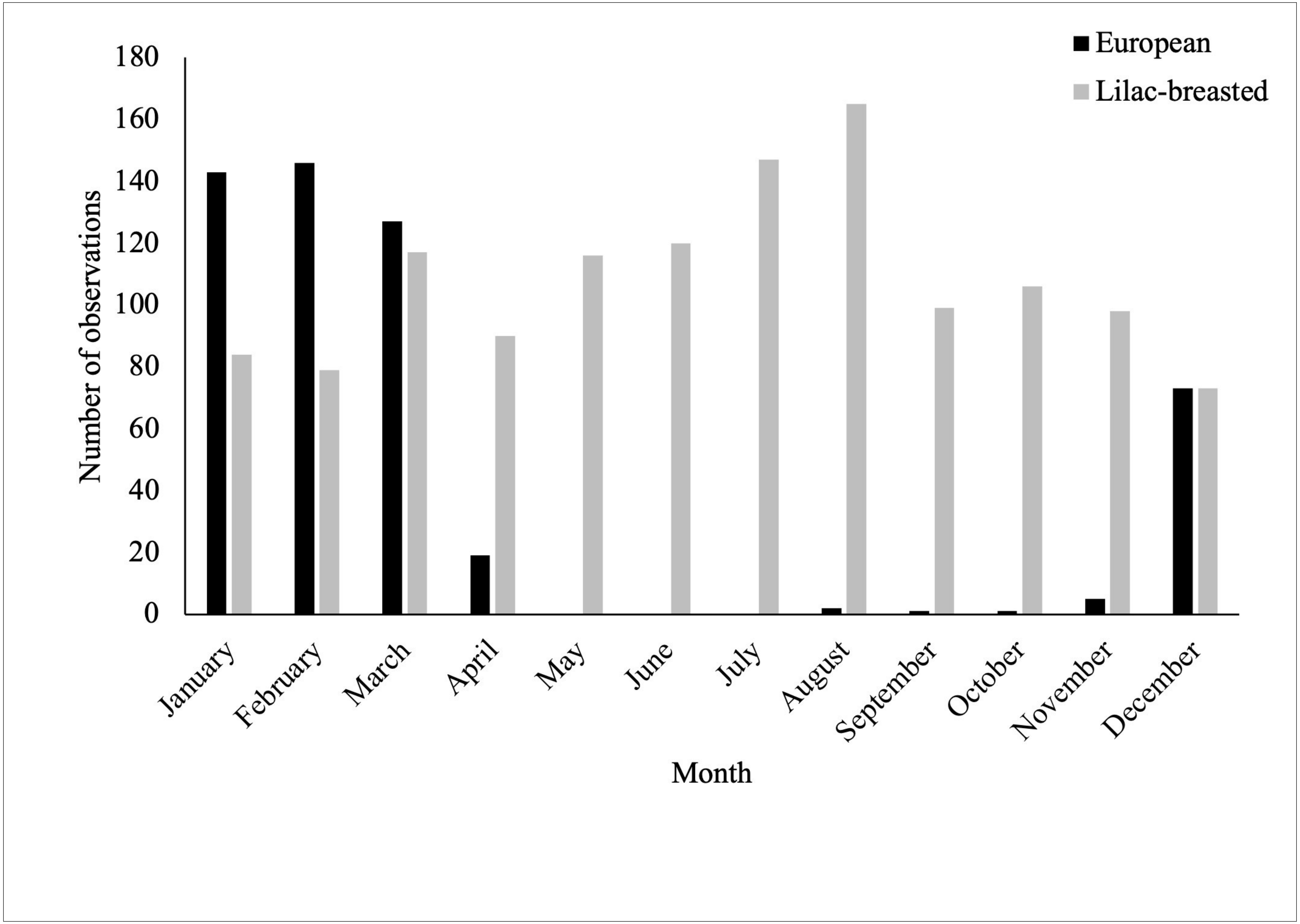

Figure 12: The number of total observations in each month for Lilac-breasted and European Rollers in southern Africa, taken from iNaturalist.

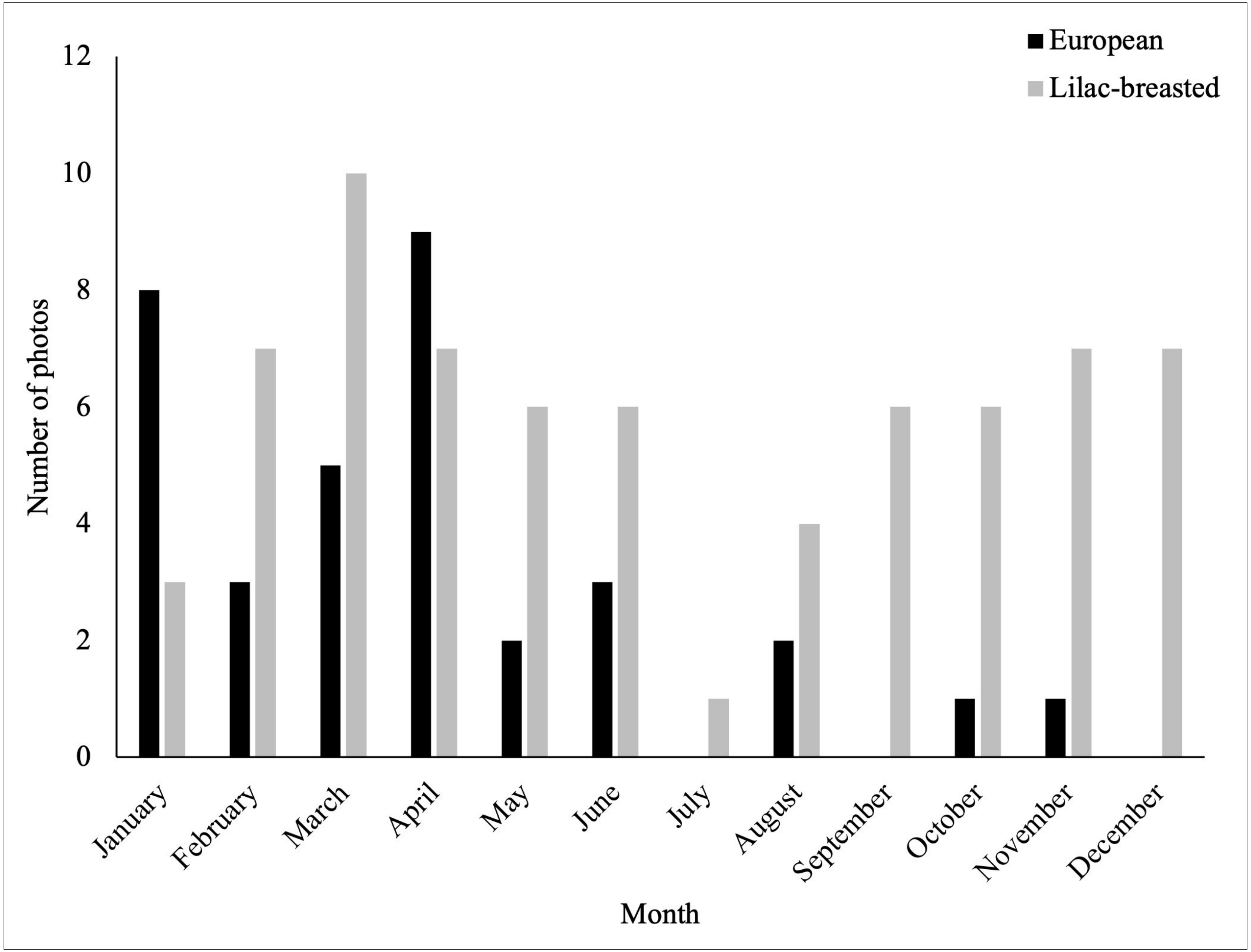

Figure 13: Frequency of Instagram photos of European (n = 34) and Lilac-breasted (n = 70) Rollers in southern Africa for each month in 2021.

source partitioning as a response to interspecific competition between this sister species pair. We have additionally highlighted the feasibility of using social media to answer ecological questions about avian diets. Future studies should incorporate other web-based photographic sources, such as Morphic (https://morphs.io, Leighton et al. 2016) which extracts photos from Google Images. In addition, these methods should be used to study a wider range of roller species, across a greater proportion of their ranges in Africa and Europe, and across a longer time range. We suggest investigating differences and shifts European Roller diets in their breeding range and home range. Additional investigation into prey characteristics such as size, nutritional quality, and noxiousness may offer insight into how resident and migratory species alleviate interspecific competition when they coexist.

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Appendix 1: Percentage of Lilac-breasted Roller diet by prey order for an invasive study by Kopij et al. (2000) and our non-invasive study.

	Lilac-breasted Roller diet by prey order (%)	
	Kopij et al. (2000)	**Our study**
Anura (frogs and toads)	-	3.5
Araneae (spiders)	6.6	2.4
Blattodea (cockroaches)	3.3	-
Coleoptera (beetles)	27.9	20.1
Eulipotyphla (hedgehogs, shrews, moles, and others)	-	0.4
Hemiptera (bugs)	-	1.2
Heteroptera (true bugs)	9.8	-
Hymenoptera (sawflies, wasps, bees, and ants)	-	1.2
Isoptera (termites)	29.5	-
Lepidoptera (moths, butterflies)	-	3.1
Mantodea (mantids)	-	3.5
Odonata (dragonflies, damselflies)	-	1.2
Orthoptera (grasshoppers, locusts, crickets, katydids)	23	43.3
Scolopendromorpha (centipedes)	-	7.5
Scorpiones (scorpions)	-	6.3
Solifugae (sun spiders)	-	2.8
Spirostreptida (millipedes)	-	0.8
Squamata (squamates)	-	2.8

Appendix 2: Percentage of European Roller diet by prey order for an invasive study by Catry et al. (2019) and our non-invasive study.

	European Roller diet by prey order (%)	
	Catry et al. (2019)	Our study
Anura (frogs and toads)	-	3.5
Araneae (spiders)	-	2.4
Coleoptera (beetles)	82.61	20.1
Dermaptera (earwigs)	5.01	-
Diplopoda (millipedes)	0.35	-
Eulipotyphla (hedgehogs, shrews, moles, and others)	-	0.4
Gastropoda (gastropods)	0.42	-
Hemiptera (bugs)	1.27	1.2
Hymenoptera (sawflies, wasps, bees, and ants)	6.42	1.2
Lepidoptera (butterflies and moths)	0.07	3.1
Mantodea (mantids)	-	3.5
Odonata (dragonflies and damselflies)	-	1.2
Orthoptera (grasshoppers, locusts, crickets, katydids)	2.54	43.3
Scolopendromorpha (centipedes)	-	7.5
Scorpiones (scorpions)	0.07	6.3
Solifugae (sun spiders)	0.49	2.8
Spirostreptida (millipedes)	-	0.8
Squamata (squamates)	0.49	2.8
Diptera (flies)	0.21	-

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Appendix 3: A selection of photos of European and Lilac-breasted Rollers illustrating each of the prey orders observed.

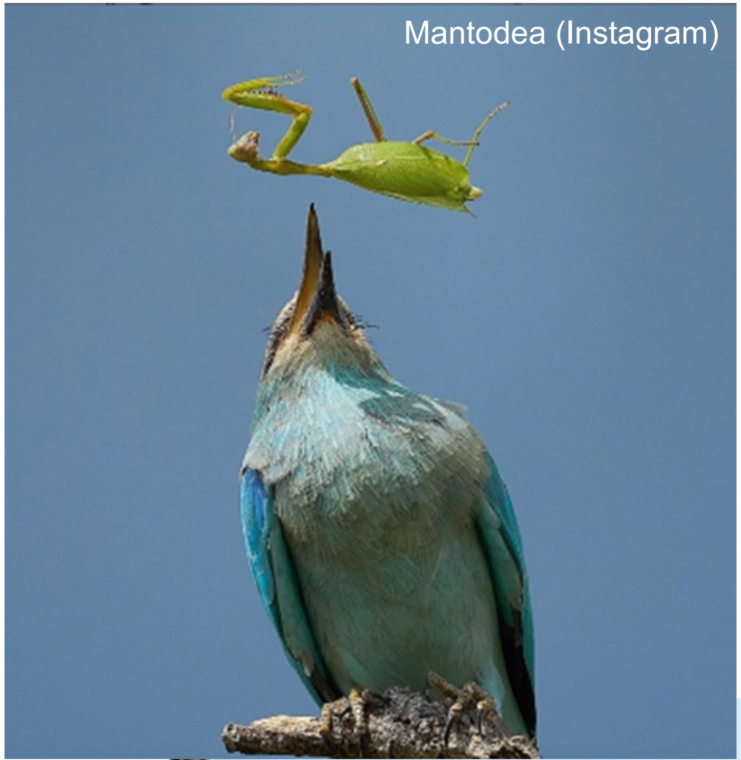
Hymenoptera (Instagram)

Coleoptera (Instagram)

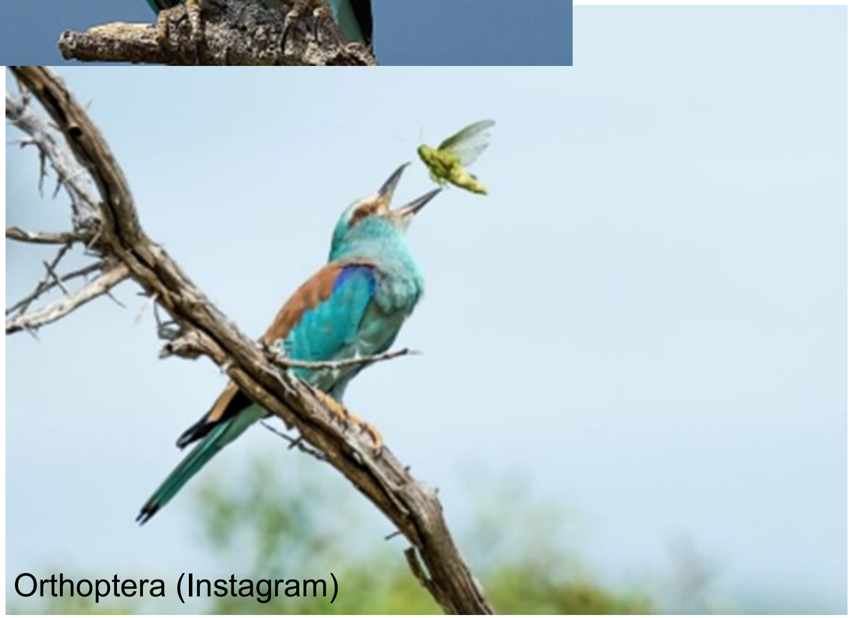
Anura (Instagram)

Araneae (Instagram)

Appendix 3 continued: A selection of photos of European and Lilac-breasted Rollers illustrating each of the prey orders observed.


Mantodea (Instagram)


Lepidoptera (Instagram)


Orthoptera (Instagram)


Scolopendromorpha (Instagram)

Appendix 3 continued: A selection of photos of European and Lilac-breasted Rollers illustrating each of the prey orders observed.

Serpentes (Instagram)


Scorpiones (Instagram)


Solifugae (Instagram)

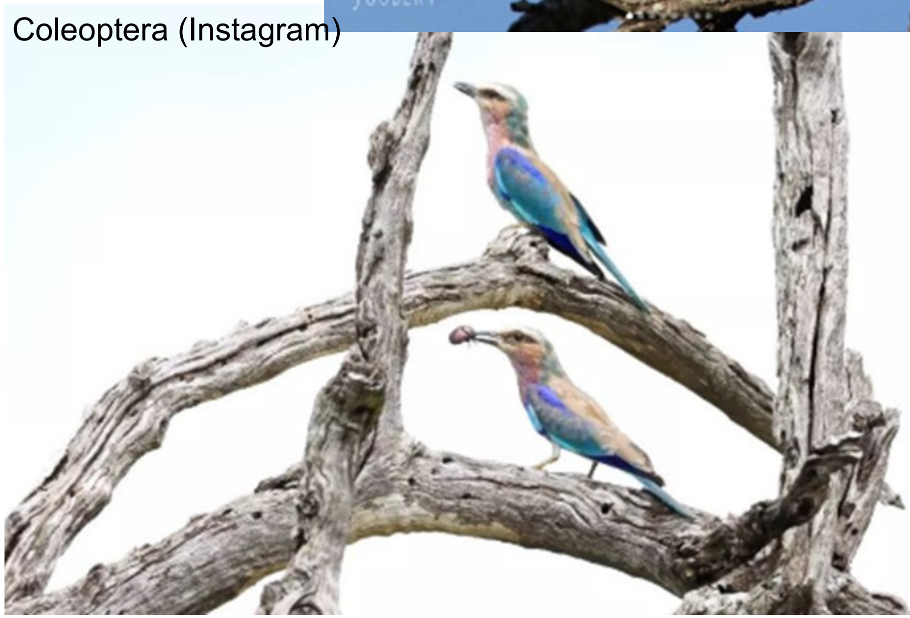

Anura (Road Transect)

Appendix 3 continued: A selection of photos of European and Lilac-breasted Rollers illustrating each of the prey orders observed.

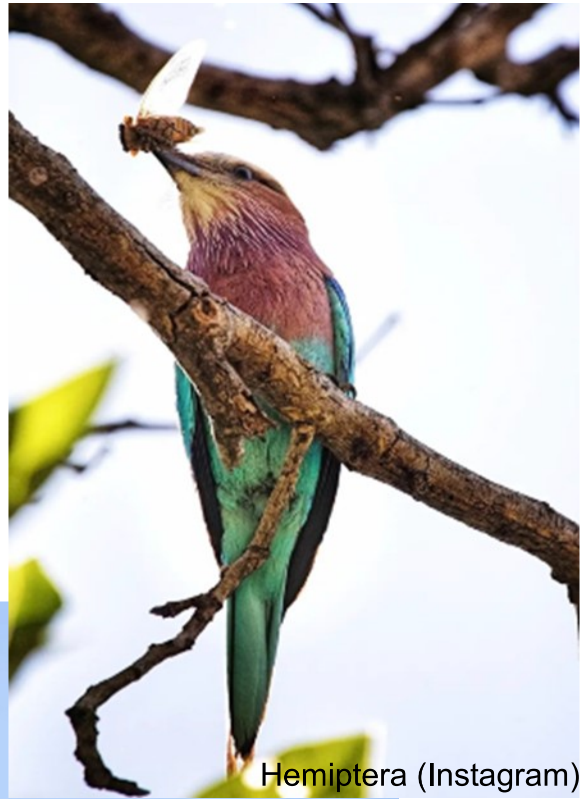

Araneae (Instagram)

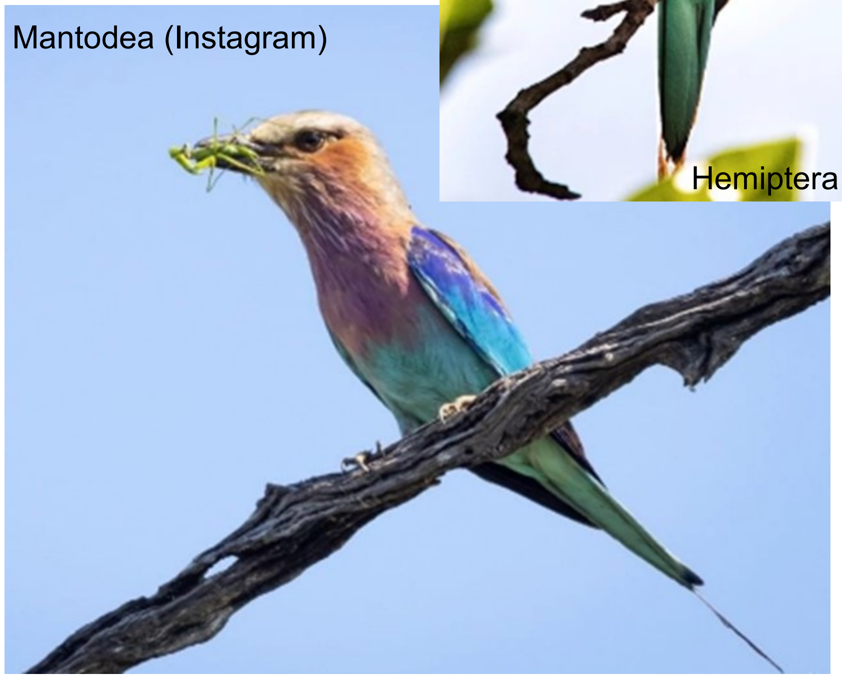
Anura (Instagram)


Eulipotyphla (Instagram)


Coleoptera (Instagram)

Appendix 3 continued: A selection of photos of European and Lilac-breasted Rollers illustrating each of the prey orders observed.





Biodiversity Observations (2023) 13: 61-94

Appendix 3 continued: A selection of photos of European and Lilac-breasted Rollers illustrating each of the prey orders observed.

Lacertoidea (Instagram)

Scolopendromorpha (Road Transect)

Orthoptera (Instagram)

Scolopendromorpha (Instagram)

Appendix 3 continued: A selection of photos of European and Lilac-breasted Rollers illustrating each of the prey orders observed.

Spirostreptida (Instagram)

Scorpiones (Instagram)

Serpentes (Instagram)