


## Opinion

## Austral birds offer insightful complementary models in ecology and evolution

Jörn Theuerkauf <sup>1,\*</sup> Camila P. Villavicencio <sup>2</sup> Nicolas M. Adreani <sup>3,4,@</sup> Alfredo Attisano <sup>1</sup> Adrian Craig <sup>5</sup> Pietro B. D'Amelio <sup>6,@</sup> Roman Gula <sup>1</sup> Alan T.K. Lee <sup>6,7,8,@</sup> Lucía Mentésana <sup>4</sup> Petra Quillfeldt<sup>9</sup> Veronica Quirici<sup>10,@</sup> René Quispe<sup>11,12</sup> Rodrigo A. Vásquez<sup>2,13</sup> John C. Wingfield<sup>14</sup> and Juan F. Masello <sup>9,\*</sup>

**The Southern Hemisphere differs from the Northern Hemisphere in many aspects. However, most ecological and evolutionary research is conducted in the Northern Hemisphere and its conclusions are extrapolated to the entire globe. Therefore, unique organismal and evolutionary characteristics of the south are overlooked. We use ornithology to show the importance of including a southern perspective. We present examples of plumage pigmentation, brood-parasitic nestling ejection, flightlessness, female song, and female aggression modulated by progesterone as complementary models for investigating fundamental biological questions. More research in the Southern Hemisphere, together with increased cooperation among researchers across the hemispheres and within the Southern Hemisphere, will provide a greater global outlook into ecology and evolution.**

## Differences between the hemispheres

Only about one-fifth of the Southern Hemisphere is covered by land compared with twice as much in the Northern Hemisphere. Yet, the Southern Hemisphere supports a disproportionately rich biodiversity [1]. Nevertheless, a recent study revealed that the number of papers published in ecology during 1996-2019 was disproportionately skewed to institutions of the Northern Hemisphere [2]. This bias was not explained by economic variables and the possibly complex factors underlying the pattern remain unclear [2]. To detect potentially recent changes in this trend, we conducted a similar analysis but focused on the study area instead of the institution. The great majority of primary research papers published in 2021 in ecology and evolutionary biology were based on research carried out in the Northern Hemisphere (Figure 1). This bias exists across all taxonomic groups considered. Despite this, conclusions have often been extrapolated to the Southern Hemisphere, even though ecological and evolutionary processes do not necessarily operate similarly in both hemispheres. This paucity of studies conducted in the Southern Hemisphere has led to biased interpretations in the past, as we detail later, and hinders our understanding of global or latitudinal patterns of biodiversity [3,4]. Furthermore, it poses problems for conservation, as an under-representation of Southern Hemisphere threatened species hinders the effectiveness of management actions [5].

The uniqueness of the Southern Hemisphere is, in part, due to its geological history. The break up of the Gondwana supercontinent about 180-160 million years ago [6] deeply influenced the biogeography and evolutionary pathways of the organisms that originated and diversified in the area. A huge number of oceanic islands formed in the Southern Hemisphere and offered opportunities for taxonomic and ecological diversification. New insights into the biology of southern

## Highlights

In ecological studies sampling must be stratified to ensure a sample population that best represents the entire population studied.

Meta-analyses assessing global patterns should also use a stratified data structure to ensure unbiased results.

We show that this is generally not the case, as individual studies are heavily biased toward the Northern Hemisphere.

We also show that Southern Hemisphere birds offer insightful complementary models for ecological and evolutionary biology.

We therefore point to the need for promoting research in the Southern Hemisphere to tackle fundamental questions with a global perspective.

<sup>1</sup>Museum and Institute of Zoology, Polish Academy of Sciences, 00-679 Warsaw, Poland

<sup>2</sup>Institute of Ecology and Biodiversity, Department of Ecological Sciences, Faculty of Sciences, University of Chile, 7800003 Santiago, Chile

<sup>3</sup>KLF Core Facility for Behaviour and Cognition, University of Vienna, 4645 Grünau im Almtal, Austria

<sup>4</sup>Max Planck Institute for Ornithology, 82319 Seewiesen, Germany

<sup>5</sup>Department of Zoology and Entomology, Rhodes University, Makhanda 6140, South Africa

<sup>6</sup>FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7701, South Africa

<sup>7</sup>Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, Scottsville 3209, South Africa

<sup>8</sup>BirdLife South Africa, Pinetown 2123, South Africa

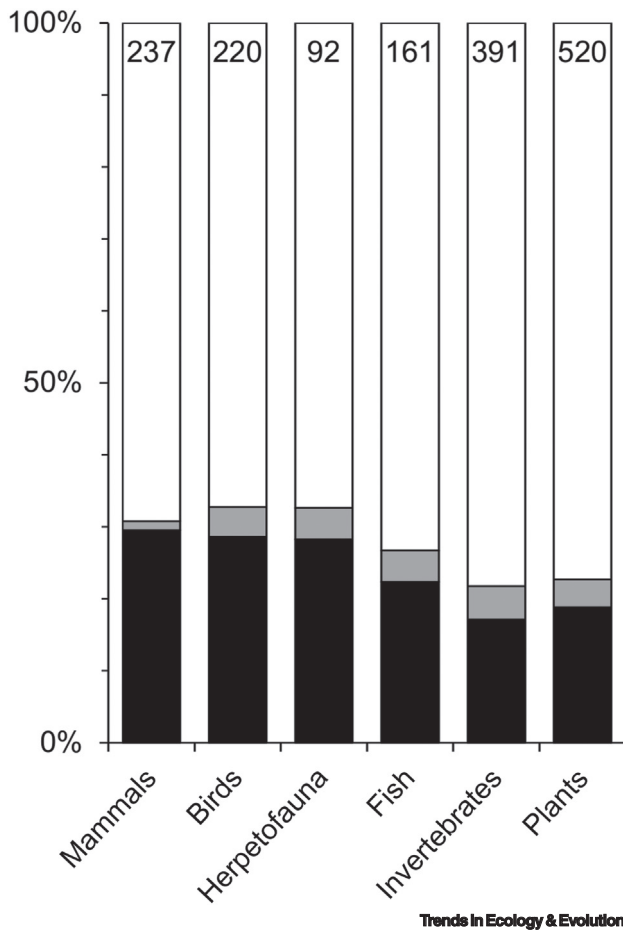


Figure 1. Proportion of primary research papers published in 2021 ( $n = 1495$ ) in high impact-factor (>5) journals in the Web of Sciences categories for ecology and evolutionary biology that include research conducted in the Northern Hemisphere (white area), Southern Hemisphere (black area), or across hemispheres (gray area). We considered only research articles with fieldwork conducted in field sites allowing a clear assignment to hemispheres (we assigned studies with single sites near the equator either to the N or S) and excluded reviews, meta-analyses, and microbial studies, as well as studies conducted exclusively in laboratories, zoos, or gardens. To qualify as cross-hemisphere study, at least one study site had to fall entirely within each hemisphere. We counted each paper only once for the most relevant organism group. Numbers in bars are the sample size (i.e., number of scientific papers) for each group.

<sup>9</sup>Department of Animal Ecology and Systematics, Justus Liebig University Giessen, 35392 Giessen, Germany  
<sup>10</sup>Centro de Investigación para la Sustentabilidad, Facultad de Ciencias de la Vida, Universidad Andres Bello, 8370251 Santiago, Chile  
<sup>11</sup>Department of Marine Biology, Faculty of Ocean Sciences, Universidad Católica del Norte, 1781421 Coquimbo, Chile  
<sup>12</sup>Department of Animal Biological Sciences, Faculty of Veterinary Sciences, University of Chile, 8820808 Santiago, Chile  
<sup>13</sup>Cape Horn International Center (CHIC), Puerto Williams, Magallanes, Chile  
<sup>14</sup>Department of Neurobiology, Physiology, and Behavior, University of California, Davis, CA 95616, USA

\*Correspondence: [jtheuer@miiz.eu](mailto:jtheuer@miiz.eu) (J. Theuerkauf) and [juan.f.masello@bio.uni-giessen.de](mailto:juan.f.masello@bio.uni-giessen.de) (J.F. Masello).  
<sup>9</sup>Twitter: @NMadreani (N.M. Adreani), @bluehillescape (A.T.K. Lee), @ornitho\_pie (P.B. D'Amelio), @LoroBarranquer2 (J.F. Masello), and @QuiriciVeronica (V. Quirici)

organisms, particularly birds, improved previous perspectives based on generalizing findings from the Northern Hemisphere. Unique evolutionary processes occur in parrots, flightless birds, and some passerines. Moreover, avian life history traits are not equally distributed between the two hemispheres, resulting in different evolutionary processes. For example, the vast majority of birds studied in the Northern Hemisphere are biparental whereas there are proportionally more cooperative breeders in the Southern Hemisphere [7]. Similarly, adult survival in birds increases more strongly with latitude in the Southern than in the Northern Hemisphere [8]. We present several ornithological examples to show that birds from the Southern Hemisphere offer novel and complementary models to achieve a more global outlook on ecology and evolution.

### Evolution – plumage pigmentation

Animal coloration plays a key role in understanding animal evolution, particularly with respect to sexual selection. Studies on avian plumage coloration are classic models for investigating the information content and honesty of biological signals in the context of sexual selection [9]. Plumage coloration is mainly produced by melanins, carotenoids, and porphyrins [10], widely present in Northern Hemisphere birds. Melanins correlate with individual hormonal state [11] and with a suite of traits leading to behavioral syndromes [12], while carotenoids usually signal nutritional or health state to prospective mates [9]. This led to the view that carotenoid-based colors are reliable signals of quality in birds, and to a widespread use of this model for research

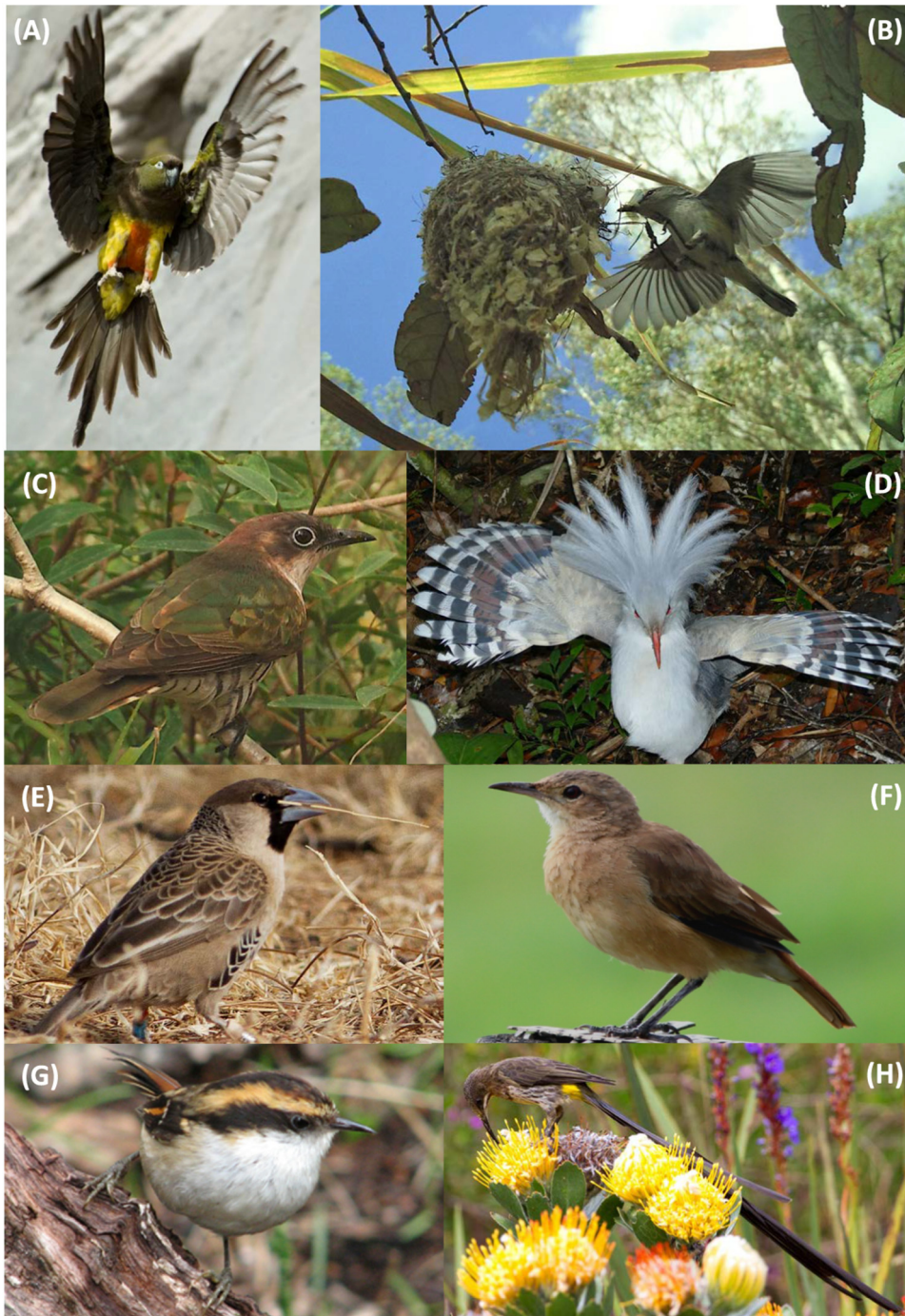
on sexual selection and mate choice [13]. However, numerous southern birds use completely different pigments, such as turacin, turacoverdin, spheniscin, vitamin A, or psittacofulvins to color their plumage [9]. The levels of psittacofulvins in burrowing parrots *Cyanoliseus patagonus* (Figure 2A) correlate with body mass, body size, body condition, sexual ornament size, sexual dichromatism, as well as parental investment, breeding success, and nestling growth [14]. Psittacofulvins are thus condition dependent and involved in a trade-off between ornamentation and immune function [14]. Since psittacofulvins might be costly to produce [15], they could also act as an honest signal of individual quality. However, contrary to carotenoids, psittacofulvins are endogenously synthesized and do not signal nutritional state or foraging ability. As different mechanisms should link psittacofulvins and individual condition, they provide a complementary model to investigate honest signaling in sexual selection and mate choice. These mechanisms and the possible costs of psittacofulvine production remain to be identified and quantified, opening possibilities for a novel research framework (see [Outstanding questions](#)).

### Evolution – brood parasitism

Decades of research on the coevolutionary arms race between brood parasites and their hosts have shown that the egg stage has a central role in well-studied systems from both the Northern and Southern Hemispheres [16,17]. This seemed to confirm earlier theoretical considerations postulating that the arms race at the nestling stage was unlikely to evolve because it should be maladaptive for the host [18]. However, host species belonging to the genus *Gerygone* in the Australasian region recognize and eject brood-parasitic *Chalcites* bronze-cuckoo chicks from their nests [19,20] (Figure 2B,C). *Gerygones* recognize the parasite nestling via acoustic and visual cues and without directly comparing it with their own chicks [21,22], which differs from other known forms of nestling rejection [23]. Furthermore, nestlings of both bronze-cuckoos and *Gerygones* present skin polymorphism [22,24]. To date, nestling ejection in the Northern Hemisphere has been found in only two unrelated bird species, which are not successfully parasitized [25,26]. Although these examples might offer a glimpse into one of the possible outcomes of the arms race (i.e., host beats parasite), they cannot contribute additional insights into the actual coevolutionary process. By contrast, the Australasian *Chalcites*–*Gerygone* systems offer unique opportunities for the study of coevolution at the nestling stage, and the life-history consequences of nestling polymorphism. First, they show that the arms race at the nestling stage can lead to different evolutionary outcomes (nestling polymorphism), which challenges our current theories and broadens our understanding of coevolutionary pathways. Second, *Gerygones* have a wide geographic distribution and are parasitized by multiple bronze-cuckoo species [27], and phylogenetic analyses suggest that nestling ejection is an ancestral trait in this group [28]. This offers a unique opportunity to study a completely different pathway of the coevolutionary arms race.

### Evolution and ecology – flightlessness and social systems

Flightless birds were once found worldwide, but with the exception of a flightless rail in the Philippines, all species in the Northern Hemisphere went extinct (e.g., the great auk *Pinguinus impennis*). The approximately 60 extant flightless bird species live, except the one mentioned previously, exclusively or mainly in the Southern Hemisphere. The loss of flight happened independently in seven taxonomic groups [29], opening new evolutionary pathways with novel behavioral and anatomical traits. The terrestrial lifestyle of flightless birds led to competition with mammals or large reptiles and promoted the evolution of gigantism, for example, in ostriches, emus, and moa, or restricted them to islands with no terrestrial mammals. Penguins (Sphenisciformes), which represent about one-third of flightless bird species, provide ideal models for investigating macroevolutionary hypotheses. Penguin wings evolved into flippers, analogous to hind flippers in seals. They have also evolved a counter-current heat exchange



**Trends in Ecology & Evolution**

Figure 2. Examples of Austral birds that offer complementary biological models to study fundamental questions in ecology and evolution. (A) Burrowing parrot *Cyanoliseus patagonus* showing its psittacofulvin-based abdominal feather patch, a signal of individual quality correlated to breeding success, nestling growth, and environmental conditions [14] (photograph: Bill Conway, deceased), (B) fan-tailed gerygone *Gerygone flavolateralis* arriving at its dome-shaped nest [20,22] (photograph: Alfredo Attisano), (C) shining bronze-cuckoo *Chalcites lucidus*, brood parasite of the

(Figure legend continued at the bottom of the next page.)

system like that of marine mammals [30]. Flightless birds, like terrestrial mammals, are confined to a mainly 2D space, meaning that they have limited dispersal ability or that they cannot easily escape predators. Therefore, flightlessness has important behavioral consequences. For example, most penguins breed and spend most of their terrestrial lives in large colonies, which led to the evolution of social interactions including advanced systems of nestling recognition by smell and voice [31]. The kagu *Rhynochetos jubatus* of New Caledonia (Figure 2D) developed a primate-like social system, with multigeneration clans of families maintained by strong social bonds [32]. Therefore, to understand how locomotion contributes to influence social systems, further studies on flightless birds are needed, and nowadays are only possible in the Southern Hemisphere.

### Bioacoustics – bird song

Bird song has generally been defined using passerine birds in northern temperate regions (with the exception of captive zebra finches *Taeniopygia guttata* from Australia): vocalizations by male birds, which serve to advertise their presence to females, and defend territory from rival males. However, this definition is inadequate for the diversity of bird song on a global scale [33]. Song by female birds has received more attention in recent years [34,35]. Plotting the occurrence of female song against phylogeny suggested that female song is ancestral in passerine birds and has been secondarily lost in some lineages [36]. For example, female red-winged starlings *Onychognathus morio* in South Africa sing regularly throughout the breeding season while male song declines [37], whereas in the New Zealand bellbird/korimako *Anthornis melanura* female singing bouts increase as male song decreases [38]. Female Australian magpies *Gymnorhina tibicen* also sing more frequently than males [39]. Such findings have led to a re-examination of assumptions about sexual selection and sexual dimorphism in birds [40,41] and show how historic and geographical research biases have led to a neglect of female song [34]. Austral birds offer a special opportunity for comparative studies of key questions: How does song acquisition differ in male and female birds? What message does song convey to the other sex? The African *Vidua* species, which are brood parasites that learn the song of their hosts and later use this as a signal to conspecifics [42], could guide new investigations of other Southern Hemisphere species. Another promising line of research is offered by suboscine birds, which mainly live in the Southern Hemisphere. Recent research showed that some suboscine birds, previously thought not to learn their songs, are capable of vocal learning [43,44]. Thus, the Southern Hemisphere offers the possibility to consider ‘song’ beyond the ‘songbirds’ and to re-examine what we know about song learning.

### Physiology – physiological mechanisms underlying behavior

Physiological traits integrate environmental and genomic information to mediate phenotypic responses [45]. These responses can have direct fitness consequences for the organisms and may potentially shape evolutionary processes [46]. However, although there have been major advances in this area, there are still open questions. One of the most fundamental gaps in our understanding of the physiological mechanisms underlying behaviors relates to the fact that almost all of our knowledge comes from studies done in the Northern Hemisphere [47]. As physiological traits are tightly responsive to environmental conditions, Austral species give us the

---

fan-tailed gerygone [19,22] (photograph: Alfredo Attisano), (D) kagu *Rhynochetos jubatus* displaying to defend the cooperative family's chick [32] (photograph: Jörn Theuerkauf), (E) sociable weaver *Philetarius socius* collecting material to build a communal nest [50] (photograph: Pietro B. D'Amelio), (F) rufous horned *Furnarius rufus*, a species in which the ratio between testosterone and progesterone appears to be related to territorial defense [48] (photograph: Natalia Allenspach), (G) thorn-tailed rayadito *Aphrastura spinicauda*, a species whose adrenocortical stress response (related to survival) does not vary among populations along a latitudinal gradient [65,66] (photograph: Rodrigo A. Vásquez), (H) Cape sugarbird *Promerops cafer*, a pollinator responsible for one of the weirdest mutualism–commensalism–parasitism relationships described [55,56] (photograph: Pietro B. D'Amelio).

opportunity to advance our knowledge by providing unexplored environments and novel adaptations. For example, Neotropical birds (e.g., Furnariidae: Figure 2F,G), with different evolutionary origins and life histories from species in the Northern Hemisphere, are useful to understand how environmental cues affect breeding and its related physiological and behavioral traits. Northern Hemisphere research suggests testosterone plays a central role in male aggression. However, in rufous horned *Furnarius rufus*, the ratio between testosterone and progesterone, and not testosterone itself, seems to be related to territorial defense [48]. The diverse breeding systems of Southern Hemisphere birds could increase our knowledge on physiological mechanisms underlying behavior. For example, in the black coucal *Centropus grillii*, a polyandrous bird with reversed sex roles, aggression in females is modulated by progesterone instead of testosterone that has been classically associated with this behavior [49]. Alternatively, in sociable weavers *Philetarius socius* (Figure 2E), which cooperate to raise offspring and build their nest structures, females ‘pay the oxidative cost of dominance’ [50], providing an opportunity to better understand how physiological mechanisms contribute to shaping cooperative behaviors and its variability [51]. Hence, research on Southern Hemisphere species offers novel physiological models to better understand how variable or flexible the physiological mechanisms underlying behavior are.

### Concluding remarks

Research in the Southern Hemisphere opens pathways to test a broad spectrum of novel hypotheses (see Outstanding questions). To show this, we presented examples from recent avian research. However, this could also be illustrated with other taxonomic groups. Australian reptiles are excellent model species for answering fundamental research questions in areas such as sexual selection, mating, cryptic female choice, sociality, reproductive effort, and signaling among many others [52]. Southern Hemisphere fish species have higher immunoreactivity than Northern Hemisphere fish [53], and Australasian plants show some form of eusociality [54] unknown from plants in the Northern Hemisphere. Moreover, the Southern Hemisphere hosts many unique ecosystems, such as islands or the South African Fynbos (Box 1), which further open new research possibilities.

There are many possible reasons why research in the Southern Hemisphere often produces results different from those of that done in the Northern Hemisphere as we demonstrated earlier.

#### Box 1. Unique biomes and biological interactions

South Africa is home to a unique biome, the richest and smallest of the world’s six floral kingdoms: the Fynbos. Part of the Cape Floristic region hotspot, the region boasts 9000 plant species in a region the size of Portugal, most of which are endemic. Although not considered to be diverse in terms of avifauna, the region is home to most of South Africa’s endemic bird species, including eight biome endemics. Two nectar-feeding species are disproportionately significant as pollinators: as many as a quarter of *Protea* and *Erica* species are pollinated by the nectivorous orange-breasted sunbird *Anthobaphes violacea* and Cape sugarbird *Promerops cafer* (Figure 2H) [55]. Within this biome, there are also unusual mutualisms. In one of these, the Cape sugarbird is host to the mite *Proctolaelaps vanderbergi* (which is a pollen predator), which in turn is host to another mite *Glycyphagus* sp., which is host to a *Sporothrix* fungus, the dispersal for all of which depend on the bird responsible for pollination [56]. The *Proctolaelaps* mite consumes significant amounts of pollen: so, the sugarbird is responsible for transporting a micro-ecosystem, pollination, and spread of a *Protea* pollen parasite. This example is unique and, thus, offers an alternative model to advance our understanding of mutualism–commensalism–parasitism relationships. It could also be used to investigate how trophic complexity influences the persistence of mutualism, an open ‘big question’ in ecological research [57]. In addition to birds, there are other unusual examples of coevolution from the Cape region. The seeds of *Ceratocaryum argenteum* (Restionaceae), for example, mimic the odor of herbivore dung to attract dung beetles [58]. Since the seeds are hard and the dung beetles cannot eat them, they transport and bury the seeds facilitating dispersal, which is an outstanding case of deception in plant seed dispersal. Recently, an unambiguous case of sexual deception of a beetle was recorded for this biome: male longhorn beetles (*Chorothyse hessei*, Cerambycidae) pollinate the flowers of a rare southern African orchid (*Disa forficaria*) [59]. A novel macrolide emitted by the flower strongly attracts the beetles, demonstrating a new biological function for plant macrolides as well as confirming that beetles can be exploited through sexual deception to serve as pollinators. Altogether, these examples from the Fynbos reveal some of the many distinctive ecological interactions found in the Southern Hemisphere that offer unconventional models in unique ecosystems for research into ecology and evolution.

### Outstanding questions

Does a trade-off with the immune system explain the condition dependence of psittacofulvins, turacin, turacoverdin, or spheniscin? How is the honesty of these signals in sexual selection maintained, and what are the physiological mechanisms?

Which factors promoted the parasite–host arms race at a nestling stage in the Southern Hemisphere?

Does flightlessness open evolutionary pathways to complex social systems?

How does song acquisition differ in male and female birds and which message does song convey to the other sex?

Are the relationships between physiology, behavioral phenotypes, and fitness in the Southern Hemisphere different from the Northern Hemisphere and how are the behavioral traits hormonally regulated?

**Box 2. Possible social solutions to overcome the hemisphere bias**

Present telecommunication means and social media give the opportunity to facilitate and coordinate research across distant regions, as shown by initiatives like the Parrot Researchers Group<sup>i</sup> (PRG) or the recently established Working Group Gondwanan Ornithology of the International Ornithologists' Union<sup>ii</sup>, which initiated this opinion article. Such enterprises help tackle research questions through cross-hemisphere cooperation [62,63] and could greatly increase our knowledge of the unique biological processes occurring in the Southern Hemisphere. For instance, joint research carried out by the PRG allowed to gather up-to-date information on threats affecting 192 populations of 96 Neotropical parrot species across 21 countries, to identify gaps of data for several other countries in the region, and to suggest priorities for conservation [60]. International journals can also help promote research from the Southern Hemisphere through effective measures such as: (i) an open recruitment call for Associate Editors, which facilitates an increase in geographic representation and consequently a diversification of the reviewers, (ii) making subscriptions affordable, even for low-income countries, (iii) taking part in existing programs that provide institutions in lower-income countries with online access to academic content, and (iv) reducing the time to which content becomes free to read [64]. Finally, research funding schemes should also promote a global understanding of ecology and evolution. The Southern Hemisphere funding schemes should prioritize and allocate more resources to within-hemisphere cooperation projects and to the exchange of scientists among its different regions. The Northern Hemisphere funding agencies should also facilitate, even prioritize and fund, research projects conducted in cooperation with scientists of the Southern Hemisphere. This will help to alleviate the lack of funding and infrastructure, often due to colonial legacies that contributed to the hemisphere research bias.

One aspect might be the breakup of Gondwana, which led to many separated islands in the Southern Hemisphere. By contrast, the Northern Hemisphere has been interconnected most of the time. While we cannot conclusively determine why the differences exist, we argue that limiting research mainly to the Northern Hemisphere will limit our ability to discover general biological principles. In individual ecological studies, sampling should be stratified to ensure a representative study. If we do not apply the same logic when tackling global questions, we will end up with biased data leading to wrong conclusions. Moreover, this imbalance hampers the improvement of management strategies, as for example, in the case of interhemispheric migrations of birds and marine species [60]. We therefore point to the need for promoting research in the Southern Hemisphere to tackle fundamental questions with a global perspective. Most research institutes are located in temperate zones of the Northern Hemisphere and ecological research, especially long-term studies, is biased toward these locations [5]. At the same time, long-term research in areas where researchers are not permanently based can be challenging due to economical limitations or cultural conflicts [61]. Possible solutions might be to foster cooperation and networking across the two hemispheres, to increase collaboration among researchers within the Southern Hemisphere, and to prioritize funding of research projects in the Southern Hemisphere and across hemispheres (Box 2). We envision a future when joint research among South American, Southern African, Australasian, and Pacific researchers will allow us to understand the processes generating the great biodiversity of the Southern Hemisphere. Investigating global change requires a global perspective. Research in the Southern Hemisphere is an essential part in such an endeavor.

**Acknowledgments**

J.T., A.A., and R.G. received funding from the National Science Centre Poland (2011/01/M/NZ8/03344, 2016/23/B/NZ8/03082, 2018/29/B/NZ8/02312), C.P.V. from FONDECYT (3160679), A.C. from Rhodes University, P.B.D'A. from the South African Claude Leon Postdoctoral Fellowship 2019–2020, R.Q. from FONDECYT (3170936) ANID-Chile, and R.A.V. from AFB-170008-CONICYT-Chile and CHIC-ANID PIA/BASAL PFB210018-Chile. We thank K.C. Burns, A.E.A. Stephens, and anonymous reviewers for useful comments.

**Declaration of interests**

No interests are declared.

**Resources**

<sup>i</sup>[www.parrotresearchersgroup.org](http://www.parrotresearchersgroup.org)

<sup>ii</sup>[www.internationalornithology.org/gondwanan-ornithology](http://www.internationalornithology.org/gondwanan-ornithology)

## References

1. Freeman, B.G. and Pennell, M.W. (2021) The latitudinal taxonomy gradient. *Trends Ecol. Evol.* 36, 778–786
2. Nuñez, M.A. *et al.* (2021) Making ecology really global. *Trends Ecol. Evol.* 36, 766–769
3. Kennedy, P. *et al.* (2017) Deconstructing superorganisms and societies to address big questions in biology. *Trends Ecol. Evol.* 32, 861–872
4. Hays, G.C. *et al.* (2016) Key questions in marine megafauna movement ecology. *Trends Ecol. Evol.* 31, 463–475
5. Christie, A.P. *et al.* (2021) The challenge of biased evidence in conservation. *Conserv. Biol.* 35, 249–262
6. Jokat, W. *et al.* (2003) Timing and geometry of early Gondwana breakup. *J. Geophys. Res. Solid Earth* 108, 2428
7. Cockburn, A. (2020) Chapter six - Can't see the "hood" for the trees: can avian cooperative breeding currently be understood using the phylogenetic comparative method? In *Advances in the Study of Behavior* (Naguib, M. *et al.*, eds), pp. 243–291, Academic Press
8. Beauchamp, G. (2021) Do avian species survive better on islands? *Biol. Lett.* 17, 20200643
9. Hill, G.E. and McGraw, K.J. (2006) *Bird Coloration*, Harvard University Press
10. Galván, I. *et al.* (2019) Unique evolution of vitamin A as an external pigment in tropical starlings. *J. Exp. Biol.* 222, jeb205229
11. McGraw, K.J. *et al.* (2002) Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *J. Exp. Biol.* 205, 3747–3755
12. Ducrest, A.-L. *et al.* (2008) Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends Ecol. Evol.* 23, 502–510
13. Carballo, L. *et al.* (2020) Body size and climate as predictors of plumage colouration and sexual dichromatism in parrots. *J. Evol. Biol.* 33, 1543–1557
14. Masello, J.F. *et al.* (2008) Is the structural and psittacofulvin-based colouration of wild burrowing parrots *Cyanoliseus patagonicus* condition dependent? *J. Avian Biol.* 39, 653–662
15. McGraw, K.J. and Nogueira, M.C. (2005) Distribution of unique red feather pigments in parrots. *Biol. Lett.* 1, 38–43
16. Soler, M. (2017) *Avian Brood Parasitism: Behaviour, Ecology, Evolution and Coevolution*, Springer International Publishing
17. Fiorini, V.D. *et al.* (2019) Obligate brood parasitism on Neotropical birds. In *Behavioral Ecology of Neotropical Birds* (Reboreda, J. *et al.*, eds), pp. 103–131, Springer
18. Lotem, A. (1993) Learning to recognize nestlings is maladaptive for cuckoo *Cuculus canorus* hosts. *Nature* 362, 743–745
19. Tokue, K. and Ueda, K. (2010) Mangrove gerygones *Gerygone laevigaster* eject little bronze-cuckoo *Chalcites minutillus* hatchlings from parasitized nests. *Ibis* 152, 835–839
20. Sato, N.J. *et al.* (2015) Nestling polymorphism in a cuckoo-host system. *Curr. Biol.* 25, R1164–R1165
21. Noh, H.-J. *et al.* (2018) True recognition of nestlings by hosts selects for mimetic cuckoo chicks. *Proc. R. Soc. B Biol. Sci.* 285, 20180726
22. Attisano, A. *et al.* (2021) Discrimination and ejection of eggs and nestlings by the fan-tailed gerygone from New Caledonia. *Curr. Zool.* 67, 653–663
23. Grim, T. (2017) Host defences against brood parasite nestlings: theoretical expectations and empirical evidence. In *Avian Brood Parasitism: Behaviour, Ecology, Evolution and Coevolution* (Soler, M., ed.), pp. 539–556, Springer International Publishing
24. Langmore, N.E. *et al.* (2011) Visual mimicry of host nestlings by cuckoos. *Proc. R. Soc. B Biol. Sci.* 278, 2455–2463
25. Yang, C. *et al.* (2015) Nestling recognition in red-rumped and barn swallows. *Behav. Ecol. Sociobiol.* 69, 1821–1826
26. Huo, J. *et al.* (2018) Russet sparrows spot alien chicks from their nests. *Avian Res.* 9, 12
27. Payne, R.B. (2005) *The Cuckoos*, Oxford University Press
28. Nyári, Á.S. and Joseph, L. (2012) Evolution in Australasian mangrove forests: multilocus phylogenetic analysis of the Gerygone warblers (Aves: Acanthizidae). *PLoS One* 7, e31840
29. Mitchell, K.J. *et al.* (2014) Ancient DNA reveals elephant birds and kiwi are sister taxa and clarifies ratite bird evolution. *Science* 344, 898–900
30. Kelley, N.P. and Pyenson, N.D. (2015) Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene. *Science* 348, aaa3716
31. Coffin, H.R. *et al.* (2011) Odor-based recognition of familiar and related conspecifics: a first test conducted on captive Humboldt penguins (*Spheniscus humboldti*). *PLoS One* 6, e25002
32. Theuerkauf, J. *et al.* (2018) Fraternal polyandry and clannish spatial organization in a flightless island bird. *Curr. Biol.* 28, 1482–1488
33. Bonnevie, B.T. and Craig, A.J.F.K. (2018) A song for the South also: defining birdsong in global terms. *Ibis* 160, 926–928
34. Riebel, K. *et al.* (2019) New insights from female bird song: towards an integrated approach to studying male and female communication roles. *Biol. Lett.* 15, 20190059
35. Austin, V.I. *et al.* (2021) Avian vocalisations: the female perspective. *Biol. Rev.* 96, 1484–1503
36. Odom, K.J. *et al.* (2014) Female song is widespread and ancestral in songbirds. *Nat. Commun.* 5, 3379
37. Houdelier, C. *et al.* (2012) Songs of two starling species: common traits versus adaptations to the social environment. *Naturwissenschaften* 99, 1051–1062
38. Brunton, D.H. and Li, X. (2006) The song structure and seasonal patterns of vocal behavior of male and female bellbirds (*Anthornis melanura*). *J. Ethol.* 24, 17–25
39. Dutoit, M. and Ridley, A.R. (2020) Females sing more often and at higher frequencies than males in Australian magpies. *Behav. Process.* 172, 104045
40. Price, J.J. (2015) Rethinking our assumptions about the evolution of bird song and other sexually dimorphic signals. *Front. Ecol. Evol.* 3, art40
41. Webb, W.H. *et al.* (2016) Female song occurs in songbirds with more elaborate female coloration and reduced sexual dichromatism. *Front. Ecol. Evol.* 4, art22
42. DaCosta, J.M. and Sorenson, M.D. (2014) An experimental test of host song mimicry as a species recognition cue among male brood parasitic indigobirds (*Vidua* spp.). *Auk* 131, 549–558
43. Kroodsmma, D. *et al.* (2013) Behavioral evidence for song learning in the subsocial bellbirds (*Procnias* spp.; Cotingidae). *Wilson J. Ornithol.* 125, 1–14
44. Döppler, J.F. *et al.* (2021) Replay of innate vocal patterns during night sleep in subsocials. *Proc. R. Soc. B Biol. Sci.* 288, 20210610
45. Ricklefs, R.E. and Wikelski, M. (2002) The physiology / life-history nexus. *Trends Ecol. Evol.* 17, 462–468
46. Hau, M. and Goymann, W. (2015) Endocrine mechanisms, behavioral phenotypes and plasticity: known relationships and open questions. *Front. Zool.* 12, S7
47. Moore, I.T. *et al.* (2019) Tales of testosterone: advancing our understanding of environmental endocrinology through studies of neotropical birds. *Gen. Comp. Endocrinol.* 273, 184–191
48. Adreani, N.M. *et al.* (2018) Not one hormone or another: aggression differentially affects progesterone and testosterone in a South American ovenbird. *Horm. Behav.* 105, 104–109
49. Goymann, W. *et al.* (2004) Testosterone in tropical birds: effects of environmental and social factors. *Am. Nat.* 164, 327–334
50. Silva, L.R. *et al.* (2018) Females pay the oxidative cost of dominance in a highly social bird. *Anim. Behav.* 144, 135–146
51. Guindre-Parker, S. and Rubenstein, D.R. (2018) No short-term physiological costs of offspring care in a cooperatively breeding bird. *J. Exp. Biol.* 221, jeb186569
52. Van Dyke, J.U. *et al.* (2020) Australian lizards are outstanding models for reproductive biology research. *Aust. J. Zool.* 68, 168–199
53. Liang, J. *et al.* (2017) Quantitative analysis of species specificity of two anti-parvalbumin antibodies for detecting southern hemisphere fish species demonstrating strong phylogenetic association. *Food Chem.* 237, 588–596
54. Burns, K.C. *et al.* (2021) Primitive eusociality in a land plant? *Ecology* 102, e03373
55. Geerts, S. *et al.* (2020) Pollination structures plant and nectar-feeding bird communities in Cape fynbos, South Africa: implications for the conservation of plant–bird mutualisms. *Ecol. Res.* 35, 838–856



56. Theron-De Bruin, N. *et al.* (2018) Birds mediate a fungus-mite mutualism. *Microb. Ecol.* 75, 863–874
57. Hoeksema, J.D. and Bruna, E.M. (2000) Pursuing the big questions about interspecific mutualism: a review of theoretical approaches. *Oecologia* 125, 321–330
58. Midgley, J.J. *et al.* (2015) Faecal mimicry by seeds ensures dispersal by dung beetles. *Nat. Plants* 1, 15141
59. Cohen, C. *et al.* (2021) Sexual deception of a beetle pollinator through floral mimicry. *Curr. Biol.* 31, 1962–1969.e1966
60. Li, J. *et al.* (2019) Mapping wader biodiversity along the East Asian–Australasian flyway. *PLoS One* 14, e0210552
61. Seidler, R. *et al.* (2021) Confronting ethical challenges in long-term research programs in the tropics. *Biol. Conserv.* 255, 108933
62. Berkunsky, I. *et al.* (2017) Current threats faced by Neotropical parrot populations. *Biol. Conserv.* 214, 278–287
63. Masello, J.F. *et al.* (2018) Can the intake of antiparasitic secondary metabolites explain the low prevalence of hemoparasites among wild Psittaciformes? *Parasite. Vector.* 11, 357
64. Pettorelli, N. *et al.* (2021) How international journals can support ecology from the Global South. *J. Appl. Ecol.* 58, 4–8
65. Cornelius, J.M. *et al.* (2012) Coping with the extremes: stress physiology varies between winter and summer in breeding opportunists. *Biol. Lett.* 8, 312–315
66. Quirici, V. *et al.* (2014) Baseline corticosterone and stress response in the Thorn-tailed Rayadito (*Aphrastura spinicauda*) along a latitudinal gradient. *Gen. Comp. Endocrinol.* 198, 39–46