The Goffin’s cockatoo (Goffin) is known for its advanced cognitive skills in the technical domain and the ability to innovate tool use in captivity. However, until recently, there were little data on the wildlife ecology of this species. Recent fieldwork in its natural habitat, the remote Tanimbar Islands in Indonesia, revealed that wild Goffins could manufacture and use tool sets to access the embedded seed of a tropical fruit. Here, we focus on the ultimate drivers and discuss the ecological and morphological factors that might have facilitated the evolution of tool-use potential in wild Goffins, a skill so far hidden in the dense tropical forest. We argue that the remarkable tool-using behaviours observed in wild Goffins derive from their foraging ecology. Habitat features specific to small tropical islands and actions stemming from seed-shelling behaviour could also facilitate the emergence of their tool-use potential. Research in comparative cognition further highlights the need to protect the biological treasures found on remote islands.

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Introduction
Research on avian cognition sometimes reveals evidence of advanced technical skills. The Goffin’s cockatoo (Cacatua goffiniana; alternative common names: Tanimbar corella, Blushing cockatoo; indigenous Tanimbaranese name: Manik tilgnoi; hereafter: Goffin) is a psittacine (parrot) species well-known for its advanced technical problem-solving skills and an ability to innovate tool use in captivity (for a review, see [1]). However, the evolutionary drivers of the Goffins’ remarkable cognitive abilities remain largely unknown.

While previously not considered to be ‘tooling around’ in the wild [2], it was recently reported that temporarily captive wild Goffins flexibly use and manufacture sets of up to three tools of different functions to access the embedded seed matter of a tropical fruit (Cerbera manghas; indigenous Tanimbaranese name: Wawai; common name: Sea mango; hereafter: Wawai; [3]). The immediate expertise of the tool-using individuals, video recordings from outdoor feeding platforms baited with Wawai fruit, and a finding of a skinned endocarp with an inserted wooden fragment underneath a Wawai tree strongly suggest that this behaviour is unlikely to be an artefact of captivity. As the tool-use behaviour of wild Goffins was limited to few individuals, it is unlikely to occur on a species-wide level. Therefore, contrary to a recent suggestion [4], we doubt that it is based on a genetic predisposition for using specific objects as extractive tools (as was proposed for the use of stick-like tools in Woodpecker finches, Cactospiza pallida, and New Caledonian crows, Corvus moneduloides; [5]).

This discovery of tool sets in wild Goffins suggests for the first time that a psittacine species flexibly manufactures complex foraging tools, an ability that was until now only known in primates [6]. Tool sets can be considered a complex form of tool use because they require multiple types of tools for different purposes to reach a single goal [6]. In that respect, they differ from simple tool use, where only a single tool is used for a specific purpose. The behavioural complexity of tool sets presents an evolutionary and developmental challenge. The tool use of wild Goffins requires recognising the affordances of the substrate (branches) for crafting new objects, the properties of the Wawai fruit and its seeds, as well as producing and managing actions and spatial relations between objects for successful extraction [7].

Complex tool use is considered rare in the animal kingdom [5], where rarity was recently proposed to be explained by a general theoretical framework consisting of two main factors: ecology and morphology [8]. Ecologically, tool-related foraging is typically costlier than other feeding strategies. It requires extended apprentice periods, carries a higher predation risk owing to long-
last year, and is not expected to evolve if easily accessible food resources are abundant. Species’ morphology may also limit the emergence of tool use either by not allowing dexterous manipulation of objects or by making tool use redundant because of a highly adapted feeding apparatus.

Following this framework, we discuss the basic preconditions of ecology and morphology for the evolution of complex tool-use potential in wild Goffins. We argue that their foraging ecology could strongly influence the evolutionary emergence of tool use. However, it is important to emphasise that the emergence of tool use is likely the consequence of an intricate combination of ultimate and proximate factors (including cognitive and social influences on the tool-use acquisition and maintenance). We also acknowledge that our present opinion might need revision when more data on the behaviour of wild psittacines become available.

**Ecological factors**

Several environmental factors have been proposed to potentially promote the evolution of avian tool use in a foraging context (where the benefits outweigh the costs of using tools): seasonal availability of food sources, the presence of high quality food items that are difficult to access (extractive foraging hypothesis), unoccupied niches to exploit these resources, and reduced predation risk (for a review, see [2]). Additionally, the geological history of an island can influence its flora and fauna, potentially resulting in unique ecological conditions that might promote the emergence of tool-use potential in local avian species.

**Tanimbar Islands**

Goffins are endemic to the remote Tanimbar Islands in Indonesia, located between Australia and Papua New Guinea (Figure 1a). Owing to the relatively small size of their native habitat (approx. 5400 km²), Goffins can be considered a restricted-range species [9]. The Australasian region was suggested as the potential centre of psittacine evolution and radiation [10]. Overwater dispersal directly from Australia during Miocene (24–5 MY; at the time when the northward-drifting Australian continent approached the island arcs resulting from the interaction of the Pacific tectonic plates and when Australia began to dry out) was proposed as the most likely route for cockatoo colonisation of the Tanimbar Islands [10].

The Tanimbar archipelago consists mainly of quartzitic sandstones [11] and lies on the collision zone of the Indo-Australian and Eurasian tectonic plates [12–15]. Based on the youngest sediments and oldest geological deposits, the uplift of reef and limestone forming these islands can be dated to have occurred during the late Pliocene (2–3 Ma; [12]). Interestingly, molecular data on the phylogeny of Cacatuinae estimate the split of Goffins from the Western Long-billed corella (Cacatua pasitator) and the Little corella (Cacatua sanguinea) during precisely this period at 2.7 Ma [16]. Therefore, it seems likely that Goffins colonised the Tanimbar Islands early and have adapted to this remote island habitat.

The climate on the Tanimbar Islands is tropical wet and dry, determined by seasonal monsoon periods [17]. Two rainy seasons occur in December–March (West Monsoon) and May–September (East Monsoon), whereas the main dry season occurs in September–December. A short dry season additionally occurs during the shifting of wind directions in April. The exact seasonal durations do not seem consistent for each year and seem to differ in the south of the main Yamdena island [2,18], whereas the interannual variability of rainfall is high [18]. Temperatures are stable, with the mean annual temperature of 21°C (between 1977 and 2003), and the humidity typically remaining high (above 70%) throughout the year [18].

Among the Tanimbar Islands, Yamdena is the largest and is relatively flat. Its forest cover spans approximately 70%, including seasonal evergreen, dry deciduous, and moist deciduous forests (Figure 1b) [18,19]. Interestingly, Tanimbar forests were recently proposed as the last natural tropical seasonal forests in Indonesia [18]. Goffins can be observed in various habitats but are primarily encountered in the forest and agriculture fields [2,19].

A high level of bird endemism characterises the Tanimbar Islands [19,20], which might indicate local climate stability [21]. Goffins were reported to maintain a substantial population of approximately 250,000 individuals in 1995 [22], even though trapping for pet trade was widespread before international trade was banned within Appendix I of the 1994 Convention on International Trade in Endangered Species [19]. Local indigenous people were also reported sometimes to hunt Goffins for food [23]. In terms of natural predators, Goffins are potentially threatened by aerial (Brahminy kite, Haliastur indus; Varied goshawk, Tachypis hioaster; Bonelli’s eagle, Aquila fasciata) and ground (feral cats, Felidae sp.; Western Pacific monitor lizard, Varanus indicus; and the Tanimbar python, Simalia nauta) predators [23].

In terms of potential competition for food resources, there are four other psittacine species on the Tanimbar Islands: blue-streaked lorikeets (Eos reticulata; endemic), Eclectus parrot (Eclectus roratus riedeli; endemic subspecies), red-cheeked parrot (Geoffroyus geoffroyi
timorlaeensis; endemic subspecies), and great-billed parrot (Tanygnathus megalorynchos subaffinis; [24,25]). These species typically target fruit, flowers, nectar, and small seeds during foraging [26,27]. Omnivorous Torresian crows (Corvus orru) and several fruit-eating and/or nectar-eating species of bats (e.g. Western naked-backed fruit bat, Dobsonia peroni; Geoffroy’s rousette, Rousettus amplexicaudatus; [28]) also live on the islands, whereas woodpeckers are absent. Therefore, the Tanimbar Islands host various species feeding on fruit, flowers, and small seeds.

**Figure 1**

The Tanimbar Islands and undercover wild Goffins. The upper panel presents (a) the geographical location of the Tanimbar Islands; (b) an aerial view of the forest habitat. The lower panel presents inconspicuous wild Goffins during feeding in the forest, as seen from a distance (left-hand side) and in close-up (right-hand side): (c) opening a young coconut (Cocos nucifera); (d) feeding on an unripe wild maracuja (Passiflora foetida) fruit. Arrows indicate the location of the Goffin in the canopy. Photographs by Mark O’Hara.

**Foraging ecology**

Goffins are opportunistic feeding generalists as they consume a variety of partially seasonal food sources [29] and gather on ephemeral feeding sites (i.e. concentrated crops of corn or green beans available for a short time). As generalist foragers, wild Goffins face several foraging challenges. Specifically, they cannot rely on a single standard or several predictable food sources and are thus unlikely to have standardised feeding techniques. Instead, foraging generalists must constantly adjust the
employed foraging techniques to utilise their feeding morphology on various food items [30].

Psittacines with psittacid-type beaks could be considered extractive foragers by nature because they typically target seeds embedded in fruit [31]. The extractive foraging hypothesis (first proposed by Parker and Gibson in 1977) addresses the evolutionary origin and functional significance of complex tool use in nonhuman animals (for a review, see [32]). It states that intelligent tool use arose as an adaptation to extractive foraging (feeding on various seasonally and locally variable embedded food sources). It thus proposes an ecological account for the emergence of complex tool use. Similarly, extractive foraging was suggested as the basic precondition for tool innovations to occur (for a review, see [33]).

In terms of extractive foraging, wild Goffins were observed to feed on a variety of embedded food sources (e.g., young coconuts, Cocos nucifera; Figure 1c; [2]) and were even observed to be capable of digging for underground cassava roots (Manihot esculenta) in a capture-release field aviary (B.M. & M.O., personal observations). The local indigenous people suggested that such digging might be present on the agriculture fields (however, wild Goffins might also rely on wild boars first to unearth the roots; [29]). In the same field aviary, motivated individuals could extract larvae from holes in rotting tree trunks placed on the ground, by enlarging the holes after initial close inspection. They sometimes even employed a toe to probe and move the larvae within the hole (B.M. & M.O., personal observations).

Morphological factors

Goffins belong to the corella (Lismetis) subgenus of white cockatoos [34]. They are generally medium-sized (32 cm), although considered one of the smaller (approx. 300 g) cockatoo species [35,36]. The relatively smaller size likely limits their ability to crack open large and/or hard-shelled food sources, such as the woody endocarp of mature Wawai fruit. With a brain mass of approximately 8 g, they are among psittacines with a high brain neurons–pallial neurons ratio (avian pallium is a homologue of the mammalian neocortex; [37]).

In terms of lifespan, cockatoos are among the longest-living psitacine species. The evolution of the long lifespan in psittacines was suggested to be influenced by ecological factors, such as granivorous diet and living on the mainland, whereas frugivory/nectarivory diet and restriction to islands were suggested to decrease the longevity (with omnivory diet ranking between these lifestyles; [38]). Furthermore, cockatoos have a long reproductive lifespan in captivity [39]. Goffins are long-lived (up to 30 years in captivity; [40]; however, lifespans of up to 40 years have been observed; A.A. personal communication).

Multipurpose feeding apparatus

The psittacine’s beak is more flexible than in most other birds, as the upper mandible is hinged onto the skull with an additional joint instead of being part of the cranium [41]. Cockatoos generally have large beaks, and Goffins possess a general-purpose psittacid-type beak, making them ‘seed-cracking’ birds [42]. The cracking action consists of many small, fast, and precise movements in the oral cavity. Psittacines have evolved enhanced biting forces because of novel adaptations in the jaw bone structure and musculature (increased lever efficiency and the presence of adductor muscles; for a review, see [42,43]). Psittacines also have an uncoupled jaw apparatus, making them unique in their ability to move the upper and lower mandibles independently [44]. This ability is beneficial for keeping the beaks sharp by grating the two jaws together when resting (bill-honing) or allowing fine positional adjustments when processing food intraorally.

The beak is complemented by a large muscular tongue, which helps manipulate the seeds intraorally for dehusking before consumption. During the dehusking, the lower jaw applies pressure, the tongue holds the seed in place, and the upper jaw acts as an anvil. Additionally, the tongue has different surface coverings (i.e. soft undersides or the lingual nail), which reflect the different functional demands placed on its various regions. The different properties of the keratinised structures allow complex modifications of the lingual surface shape by the internal structures. Therefore, the tongue can interact in an integrated way with the environment, and its considerable mobility is an adaptation for foraging on seeds and nuts [45].

In most avian species, the tip of the beak contains multiple aggregations of sensory receptors forming a ‘bill tip organ’. This complex sensory structure is used to select and assess food items held inside the beak, and has an essential role in plumage care [46]. The sensory receptors within the organ include two types of nerve endings that correspond functionally with the mammalian mechanoreceptors. They provide information on mechanical pressure, position, shape, and edges (encoding the surface features of objects into perception), as well as sensations of fine, discriminative touch, and vibration [47,48].

Psittacines are adapted to the arboreal lifestyle and food gathering. The uniformly short legs lower their centre of gravity, which helps with stability during foraging on small branches (with the beak often acting as a third leg) and allows the head to be optimally positioned for
identification and collection of food items [10]. The zygodactyl feet with the two middle toes pointing forward and two outer toes pointing backwards provide a firmer grip than the typical arrangement among birds of three forward toes and one rear toe. The psittacine toe arrangement provides strength and dexterity (e.g. allowing hanging upside down from the branches to reach the food). The foot is used as a hand for object gripping during feeding, and the long toes can even be used for probing holes [2].

Seed-shelling behaviour
Psittacines are among birds processing food intraorally [44]. Species with a psittacid-type beak have a unique way of removing the shell and coat of seeds before swallowing them (Figure 2a). They brace a seed against the inside of the projecting upper bill tip and hold it in place with the tip of their muscular tongue, while the cutting edge of the lower mandible cuts or cracks the seed shell. The outer half of the seed shell is then separated from the kernel with the cutting edge while the tongue rotates the seed. This operation requires a fine coordination of raising and lowering the upper and lower mandibles, finely tuned sideway movements of the cutting edge of the mandible, dexterous back-and-forth, up-and-down and sideway movements of the tongue bones and connective tissues, up-and-down and small sideway movements of the tongue, as well as modifications of the lingual tip of the tongue from spoon-shaped to flat. These fine-scale actions are guided by the advanced sensory receptors inside the beak [44].

When feeding on items grasped in the foot, psittacines do not passively hold them but actively manipulate them (by turning or rotating) while processing the food item with the beak and tongue [49]. During close inspection of potential food items, objects are brought with the foot towards the binocular portion of the visual field. Once held inside the beak, the bill tip organ and the tongue provide tactile information about the objects and reduce the need for further visual cues [50]. In this way, psittacines can simultaneously collect tactile information about objects and stay vigilant against predators [50].

Discussion
Wild Goffins face the ecological circumstances and possess the morphological capability for developing tool use in their natural habitat (Figure 3). The discovery of tool use in wild Goffins further points to the tropical islands as incubators of avian tool-use potential. The psittacine beak morphology does not seem to have evolved specifically for using objects as tools, but can be instead used as a multitool in itself. The beak, being both sensitive and powerful, can be dexterously coordinated with the tongue and feet, making it an adaptive multipurpose foraging apparatus [30]. However, the tool use in wild Goffins might be considered as ‘undercover’ owing to intraoral object processing and predation pressure.

Treasure islands
The emergence of avian tool use was proposed to be facilitated by ecological conditions specific to small tropical islands, such as lower predatory pressure or reduced foraging competition for embedded food sources (e.g. no woodpeckers), leading to an opportunity for extracting these profitable food sources (for a review, see [51]).

Psittacines are considered prey animals [52] and therefore exhibit vigilance behaviours. Wild Goffins face predation risk from ground and aerial predators, including humans who might trap them on agriculture fields or hunt them in the forest. High levels of vigilance could be considered as potentially limiting the emergence of tool use. However, owing to their unique morphological adaptations, psittacines can simultaneously explore objects and observe their environment.

Interestingly, it seems that wild Goffins might face competition for easily accessible food sources, such as fruit, flowers, or small seeds. It might force them to explore other, unoccupied feeding niches containing embedded, hard-to-access food sources that Goffins could extract with their powerful multipurpose beaks. The potentially increased opportunism in wild Goffins could also explain why they are the only avian species aggregating in large flocks on local agriculture fields and visiting outdoor feeding platforms [3,19].

Tooling undercover
Despite the curvature of their beaks, psittacines are capable of highly precise manipulations by pressing objects with their dexterous tongue in a thumb-like fashion against the sensitive upper mandible [44]. Dynamic and efficient intraoral food processing, tool manufacture and handling of small wooden fragments, as well as the fact that psittacines can efficiently manipulate objects in their beak without the need of visual information make it challenging to observe tool use in the natural setting of the dense tropical forest. Moreover, Goffins display relatively high levels of vigilance behaviour because of the predation pressure they face on the Tanimbar Islands, and thus, while foraging they might often remain hidden in the protection of the thick vegetation or behave in a stealthy (quiet and cautious) way (B.M. & M.O., personal observations; Figure 1c and d).

The seed-shelling behaviour (Figure 2a) is of particular relevance to the evolution of psittacines’ tool-use potential. The required fine actions could be considered a behavioural base for developing tool manufacture,
Modification, and tool use. Indeed, adjustments of behaviours already present in a species’ repertoire were suggested to facilitate the emergence of tool use [8]. Similar to the seed-shelling behaviour, wild Goffins modify small wooden fragments into tools by turning them with the tongue inside the oral cavity (Figure 2b). This fine-tuned manufacture is followed by a repurposed handling technique where the tool is pressed against the upper mandible by the tongue (Figure 2c; instead of pressing the tool with the lower mandible, as a corvid would; [5]). Interestingly, repurposing of the tongue to hold objects against the lower mandible was also observed in a disabled kea (Nestor notabilis; [53]).

Owing to the covert characteristics of wild Goffin tool use, a purely opportunistic direct observation of this behaviour in the tropical forest would be either highly unlikely or even impossible. Indeed, the field observations conducted so far (518 hours of scanning effort resulting in 95 hours of direct observations) might not have been sufficient for uncovering tool use in the dense tropical forest. Similarly, years of intense fieldwork and focal observations were required before tool manufacture, and complex tool use was recorded in another Indonesian arboreal species, the orangutan (Pongo pygmaeus; for a review, see [54]).

**Future outlook**

Future studies should focus on investigating the spread of tool use on the Tanimbar Islands and whether Goffins are unique among cockatoos in their advanced technical abilities. Endemic birds on tropical islands that are
This study presents the discovery of complex tool use in wild Goffins. Only a few individuals were observed to be tool users, and they used two different techniques to manufacture up to three types of tools used for different purposes (tool set).

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