

Article

The Various Ways in Which Birds Blink

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Simple Summary: While our blink simply involves lowering the upper eyelid, with little involvement of the lower lid, birds have various ways of blinking depending on the species and the circumstances. Like us, they have upper and lower eyelids, though the upper lid only moves down in parrots, owls, pigeons, and a few others. The lower lid rises with drowsiness and when the bird is preening. Birds blink when they turn their heads using a ‘third eyelid’, the nictitating membrane which moves horizontally from the inner part to the outer part of the eye. The closest cousins of birds, crocodiles, blink with their lower lids and nictitating membranes but not their upper lids. As crocodiles have changed very little since they first appeared, it seems likely that their way of blinking is similar to that of the common ancestor of birds and crocodiles, the archosaur. So, upper lid blinking in birds probably came later than lower eyelid and nictitating membrane blinking. The orders of bird which have upper lid blinking are not closely related, so this type of blink is likely to be an example of convergent evolution where distantly related species evolve similar traits to adapt to similar needs. Blinking evolved as a way of keeping the cornea moist when fish first left the sea and is an as yet neglected marker of vertebrate evolution.

Abstract: There has, to date, been no systematic study of the various ways in which birds blink. Digital video recordings were made, and studied using still frames, of 524 bird species, mainly in zoos but also in the wild. Videos on 106 species from various sites on the internet were studied, some of which we had also videoed, giving a total of 591 (out of a possible 10,000) species from all 43 orders and 125 (out of a possible 249) families. Digital video recordings were also made of 15 (out of a possible 24) species of crocodile. Three types of blink were observed in birds: (1) Nictitating membrane blinks were rapid and brief (phasic) and occurred mainly on head movement. (2) Upper lid blinks were seen in parrots, owls, pigeons and some others. These were also rapid and brief and accompanied nictitating membrane blinks. (3) Lower lid blinks were slow and sustained (tonic) and occurred with drowsiness and preening. Nictitating membrane blinks and lower lid blinks were seen in crocodiles but not upper lid blinks. Globe retraction, where the eyeball is pulled into the orbit of the skull during a blink, was seen in crocodiles but not birds. Phasic blinks remove debris and moisten the cornea, essential for allowing oxygen to diffuse into the cornea, which has no blood supply. Tonic blinks are probably mainly protective. The orders of birds which have upper lid blinking are not closely related and this feature is probably the result of convergent evolution.

Keywords: nictitating membrane; eyelids; birds; avian; upper lid; lower lid; crocodiles



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1. Introduction

Blinking is of importance in an evolutionary context as it was one of the key factors which allowed fish to leave the sea and assume a terrestrial lifestyle. Most fish do not blink. They have no need to, for oxygen dissolved in water can diffuse into the epithelium on the surface of the cornea. The cornea is transparent and contains no blood vessels. Blood vessels would pose a barrier to light reaching the retina. Fish venturing from water onto land faced the problem that when the cornea dries out, atmospheric oxygen is no longer

able to diffuse into the cornea (this is why the corneas of unconscious, unblinking patients in intensive care units swell and become opaque if moisture is not frequently applied to their eyes). Blinking, sweeping moisture over the cornea with eyelids, allows atmospheric oxygen to dissolve in the fluid and diffuse into the cornea.

In mudskippers, fish which spend much of their time out of water, sea water in a cup below the stalk on which the eye sits moistens the globes when the eye retracts [1]. In longer established terrestrial vertebrates, lacrimal and Harderian glands provide tears. In birds, tears are mainly produced by the Harderian gland [2] and reach the cornea through a duct which opens into the base of the nictitating membrane. As well as moistening the cornea, tears from the Harderian gland contain antibodies which protect against infection. In humans, cats and dogs, where three layers in the tear film are described, an outer layer of mucin slows the rate of evaporation of tears and lubricates the movement of the eyelids [3,4].

Video has proved to be a useful clinical tool for observing gait, eye movement and involuntary movements [5,6] and was used in this study to investigate how birds blink. Blinking in humans can be a reflex (for example, the corneal reflex), voluntary or spontaneous [7]. While spontaneous blinking in humans is a relatively simple process, the upper lid briefly falling and rising about twelve times a minute [8], birds have more than one type of spontaneous blink, and not all species blink in the same way.

In one of the earliest accounts, Owen [9] noted that, like non-avian reptiles, birds have three eyelids. The upper and lower lids move in the vertical plane. The third, the nictitating membrane, is drawn horizontally or obliquely across the cornea by the combined action of the *quadratus membranae nictitantis* and *pyramidalis membranae nictitantis* muscles which lie behind the eyeball [10].

Owen [9] observed that the lower eyelid rises in sleep. Owls and nightjars blink with their upper lids. The upper eyelid is elevated by *levator palpebrae superioris* and the upper and lower eyelids are brought together by the action of *orbicularis oculi*. In an anatomical study, Stibbe [11] contrasted the nictitating membrane blink of birds with that of mammals. In the latter, the membrane is not actively drawn across the eye by the contraction of muscles. Rather, it lies in a state of elastic tension out of sight on the medial side of the globe, springing across when the eyeball retracts by the action of the *retractor bulbi* muscle. In birds, the muscles required for globe retraction, and in most birds for eye movements, have become vestigial—capable of causing only low-amplitude eye movement of the type, for example, which causes saccadic oscillation [12]. This evolved presumably to lighten the load for flight.

In cats and dogs, globe retraction only occurs during blinking with both eyelids, so the membrane is not usually seen. Blount [13] measured the inter-blink interval in a wide range of mammals, some reptiles and amphibia, and in four species of birds. In an eagle owl, often the blinks involving the eyelids or nictitating membrane were unilateral. Of relevance to the present study, it was noted that in a parrot, the lower lid was much slower to return to its resting position than the upper lid. Most fish do not have functioning eyelids and Blount surmised that blinking evolved in air-breathing animals as a means of preventing desiccation of the cornea by exposure to air. Mowrer [14] proposed that blinking during head movements, which are rapid and frequent in birds as they have to compensate for their lack of eye movements, might prevent blurred images reaching the retina. During rapid head turns, images traverse the retina at a rate beyond the capacity of the retinal photoreceptors to respond adequately [15]. Yorzinski [16] has more recently proposed that blinking during a gaze shift, a time when visual information is already limited, may minimise additional information loss. Kirsten and Kirsten [17] measured the spontaneous blink rates of 25 species of birds. They also noted a correlation between blinks and head turns. Nocturnal species such as owls had a lower blink rate than diurnal species. Curio [18] coined the terms ‘tonic’ and ‘phasic’ blinks to distinguish slow prolonged blinks from rapid brief ones. In the tonic blinks of many orders (Anseriformes, Accipitriformes, Falconiformes, Galliformes, Charadriiformes, Columbiformes and the Oscines suborder of Passeriformes),

the lower lid rises during sleep. In Psittaciformes and Trochili (hummingbirds), the upper lid descends in sleep and in Strigiformes and Caprimulgiformes, both lids are involved. He commented that ‘such information is lacking for most orders, or the handbooks provide wrong or conflicting information’.

The purpose of the present study was to take up Curio’s challenge and increase our understanding of the way that birds blink across the avian orders. To do this, we aimed to video or obtain videos of representative numbers of species from every order of birds to test the following hypotheses: Do all birds have the same type of blink? Is the blink type related to activities such as head turns, drowsiness, nocturnality, preening or ground feeding/pecking? Where a blink type is confined to certain species of bird, can this be related to phylogeny? How does blinking in birds compare with blinking in their closest cousins, Crocodilia?

The following predictions were made: Such has been the evolutionary flowering of birds and the myriad environments to which they have adapted, not all birds will have the same types of blink. Blinking in birds will differ from blinking in crocodilians, which have changed little since they first emerged.

2. Materials and Methods

Birds were videoed throughout the year from 2015–2021 using a Panasonic Lumix DMC FZ2500 digital single-lens reflex camera and a Sony FDR–AX53 camcorder. The zoom on these cameras allowed close-up views of the eyes even when the bird was more than 5 metres away. There was no intervention such as making a noise, gesticulating or using flash photography. Most filming was carried out at 25 frames/second and in some settings, for example, to see saccadic oscillation, at 100 frames/second. If they remained in view, birds were videoed for at least a minute. When the opportunity arose, the same bird might be videoed repeatedly. Wild birds were studied in Sydney, Australia, and to a small extent in the UK and the Netherlands. Captive birds and other animals were filmed at zoos in Australia: Taronga and Featherdale Park in Sydney, the Reptile Park in Gosford and zoos in Canberra, Melbourne, Adelaide, Launceston and Queensland (Australia Zoo, Lone Pine and Currumbin); Singapore: the Jurong Bird Park; UK: London Zoo, Whipsnade, Barnes Wetlands, Torquay, Woburn Abbey, Bristol, Crocodiles of the World in Carterton, Oxfordshire and the Suffolk Owl Sanctuary; Ireland: Dublin; Belgium: Pairi Daiza Zoo; France: ZooParc de Beauval; Netherlands: Rotterdam Zoo, the Avifauna Park; USA: Bronx Zoo in New York, San Diego Zoo; South Africa: Pretoria, Hout Bay and Stellenbosch; New Zealand: Auckland; Greece: Athens. Sampling was opportunistic depending on which species the zoos happened to have. Common species were often videoed multiple times and no major differences were ever observed between blinks in different individuals of the same species. Rare species might be videoed only once.

Digital video files were analysed using Movavi Video Editing software [Versions 12.1 to 15.4.1] (which is easy to use and not overly expensive), made in Novosibirsk, Russia, with a Dell laptop (XPS 15 9560), made in Longhua, China, and later a MacBook Pro (2.6 GHz Processor and 16 GB memory), US Apple Company, manufactured in China. Video files could be viewed frame by frame in order to follow the position of the eyelids and nictitating membrane during the course of a blink. The software has a facility for taking still pictures. Examples are shown in Figures 1–16. In order to obtain a more complete representation across the orders, videos from a further 106 species from the internet were studied. These were played back at a quarter speed, providing clear information on the positions of the eyelids and nictitating membrane during the course of the blink. Still photos were not taken. The identities of species were confirmed using the Cornell University site Birds of the World (<https://birdsoftheworld.org>).

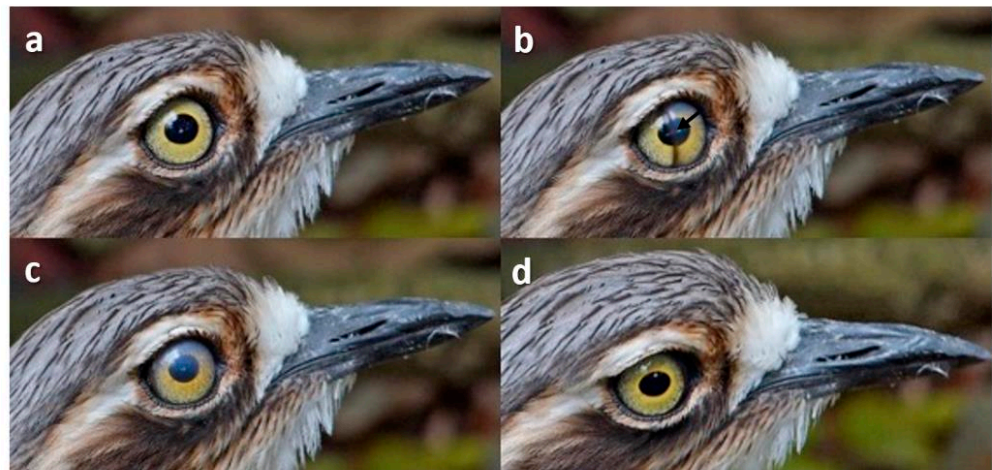


Figure 1. Nictitating membrane blink on head movement in a Bush Stone-Curlew (*Burhinus grallarius*). Sequence: (a): pre-blink; (b): transparent nictitating membrane has crossed from the medial canthus to halfway across the pupil; (c): the membrane has covered the cornea (which appears slightly opaque as a result); (d): post-blink.

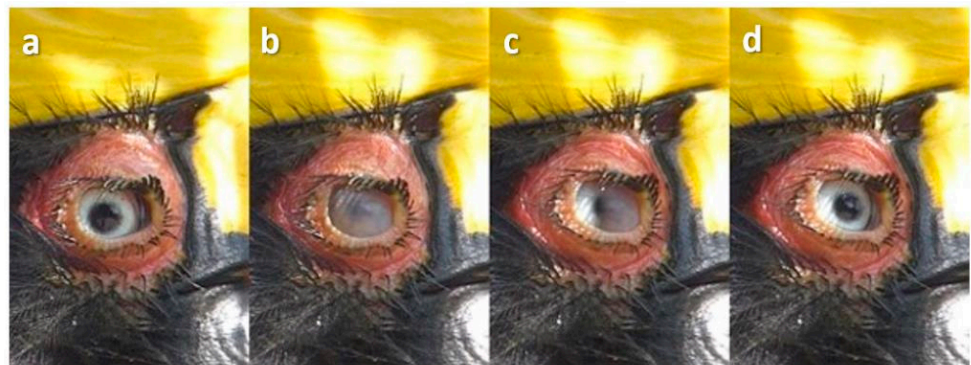


Figure 2. Nictitating membrane blink on eye movement in a rhinoceros hornbill (*Buceros rhinoceros*). Sequence: (a): pre-blink; (b): cloudy nictitating membrane has covered the cornea; (c): the membrane is moving back towards the inner canthus; (d): post-blink.

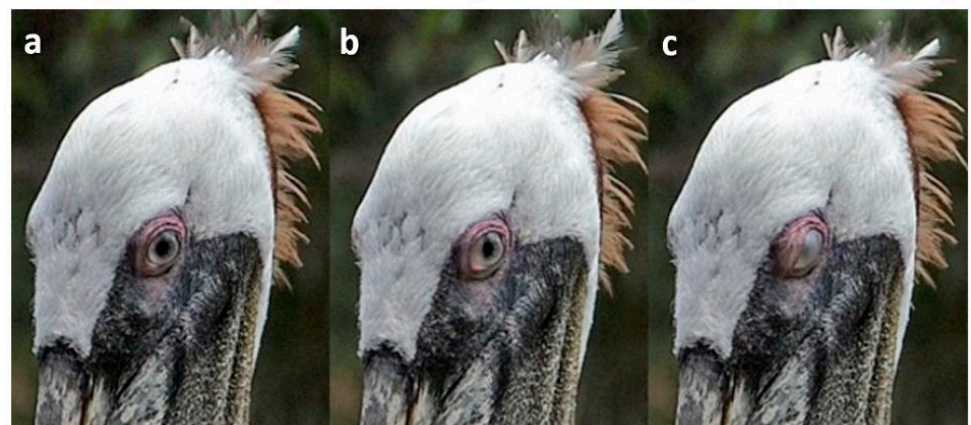


Figure 3. Nictitating membrane blink with partial upper lid blink in a Brown Pelican (*Pelecanus occidentalis*). Sequence: (a): pre-blink; (b): cloudy nictitating membrane has moved from the inner canthus to the edge of the pupil; (c): the membrane has covered the cornea and the part of the upper lid closest to the inner canthus has lowered a little.

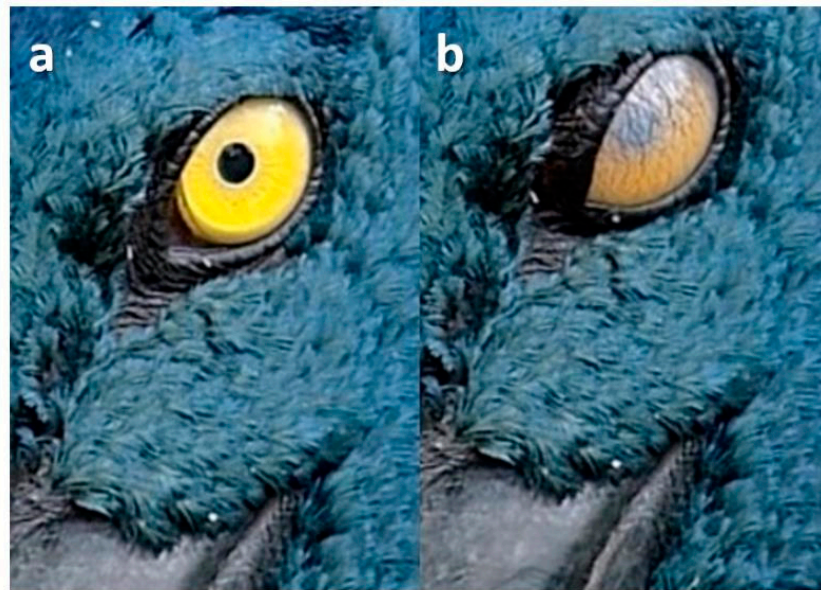


Figure 4. Nictitating membrane blink showing vascular arcades in a Black-Necked Stork (*Ephippiorhynchus asiaticus*). Sequence: (a): pre-blink; (b): blood vessels visible in the nictitating membrane during a full blink.

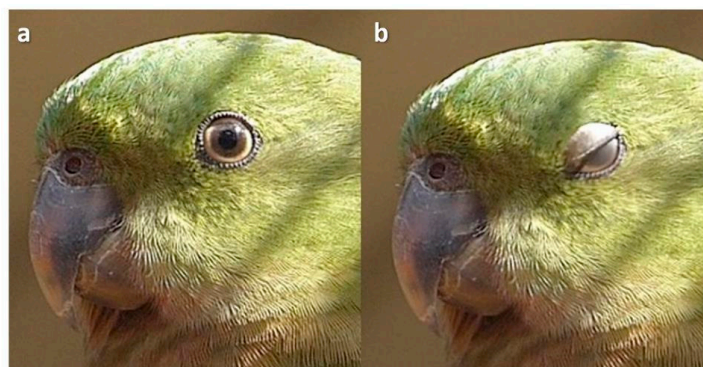


Figure 5. Upper lid and nictitating membrane blink in a female Australian King Parrot (*Alisterus scapularis*). Sequence: (a): pre-blink; (b): the upper lid is half lowered and a cloudy nictitating membrane is seen below it.

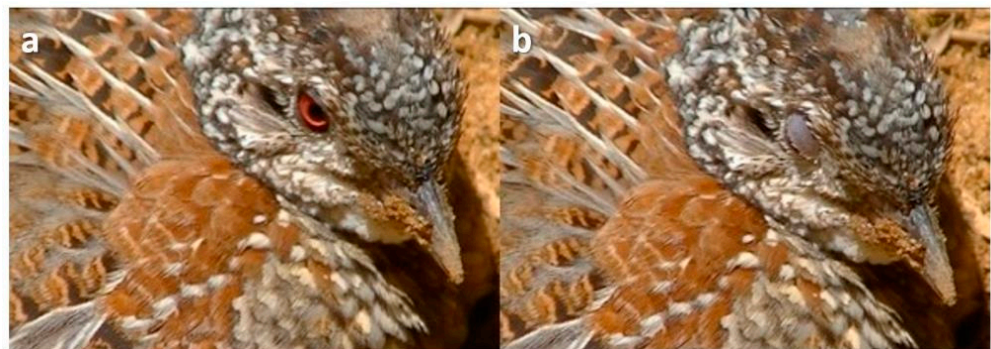


Figure 6. Upper lid blink in a Painted Buttonquail (*Turnix varius*). Sequence: (a): pre-blink; (b): full upper lid blink.



Figure 7. Lower lid elevation during preening in a Pied Imperial Pigeon (*Ducula bicolor*).

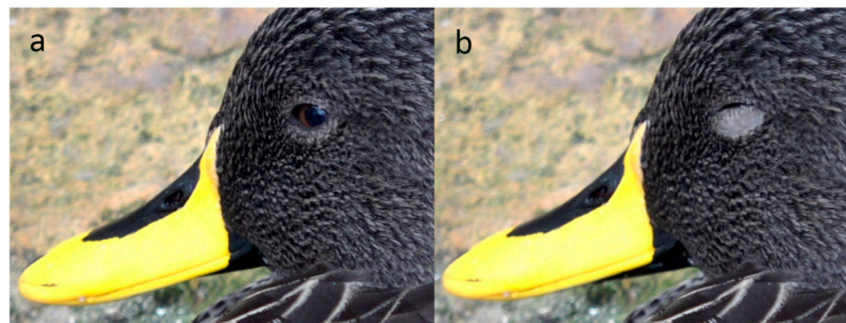


Figure 8. Lower lid elevation in a Yellow-Billed Duck (*Anas undulata*). Sequence: (a): awake; (b): asleep.

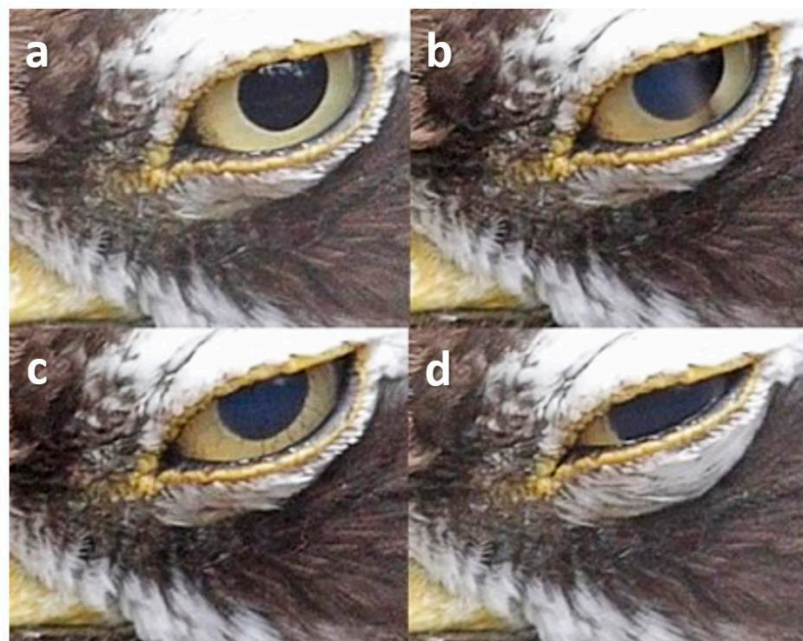


Figure 9. Nictitating membrane and lower lid blink in a Beach Stone-Curlew (*Esacus magirostris*). Sequence: (a): pre-blink; (b): transparent nictitating membrane crosses the pupil from the inner canthus; (c): membrane has covered the cornea; (d): lower lid starts to elevate, and the pupil has dilated.



Figure 10. Upper and lower lid blink during pecking in a Feral Pigeon (*Columba livia domestica*). Sequence: (a) Pre-blink; (b) Upper and lower lids come together.

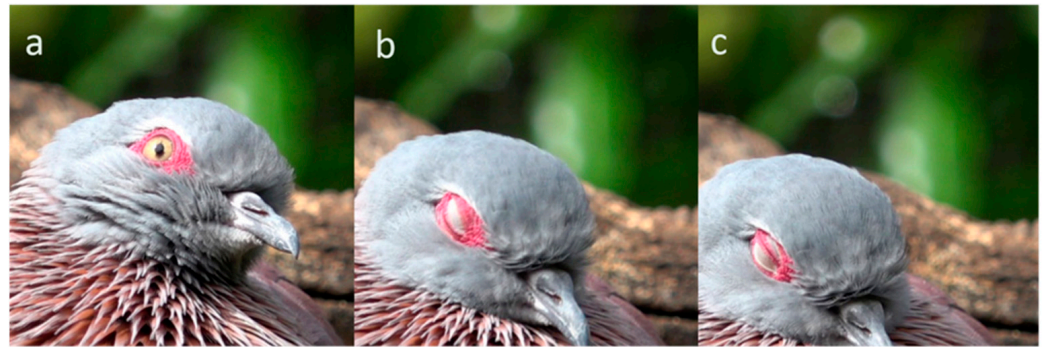


Figure 11. Synergic upper and lower lid blink in a Speckled Pigeon (*Columba guinea*). Sequence: (a): pre-blink; (b): full upper lid blink; (c): the lower lid has risen, ‘pushing’ the upper lid upwards. Both lids are pale and paper thin.

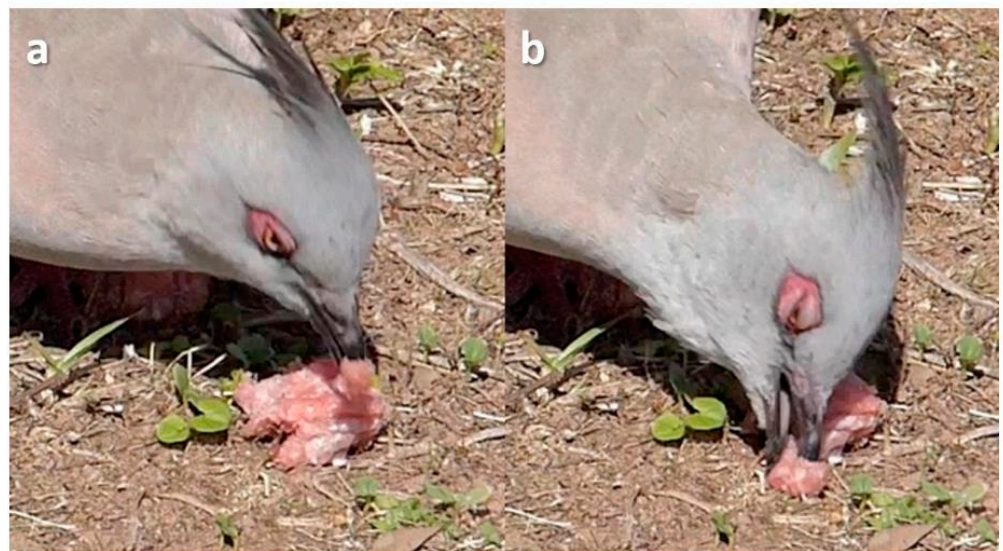


Figure 12. Squint in a Crested Pigeon (*Ocyphaps lophotes*) while pecking. (a) The upper lid starts to lower; (b) The lower lid rises leaving a slit through which the pupil is visible.



Figure 13. Squint on head turn in a Snowy Owl (*Bubo scandiacus*). (a) Pre-blink; (b) Both lids start to come together, the pupil remaining visible; (c) A small gap remains between the lids.



Figure 14. Squint in a Tawny Frogmouth (*Podargus strigoides*). (a) Pre-blink; (b) Upper lid lowers a little; (c) Lower lid rises but pupil remains visible; (d) Lids come together.

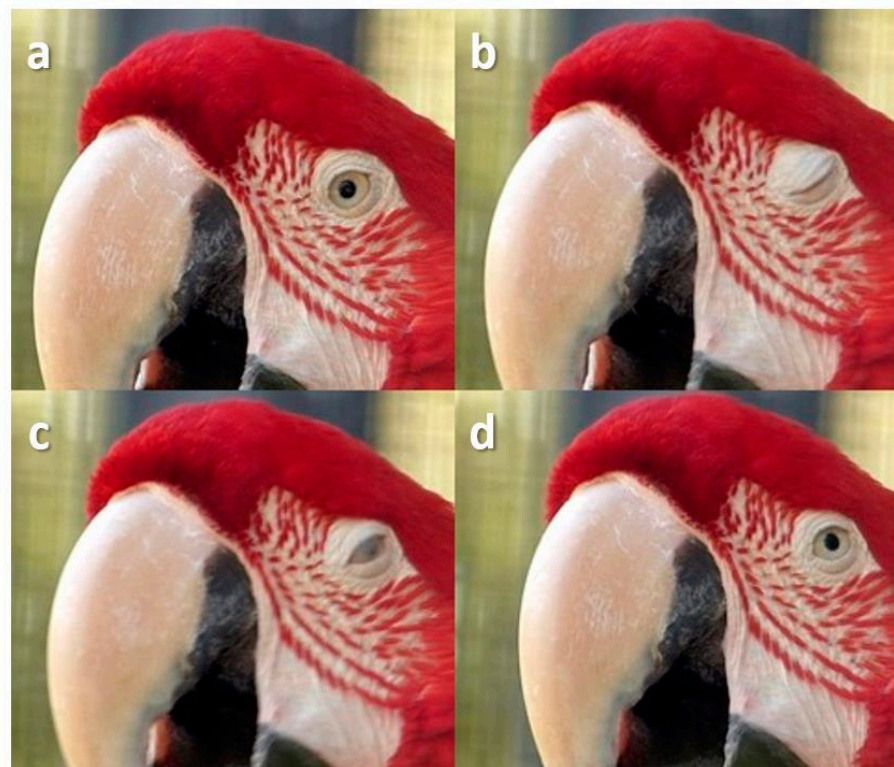


Figure 15. Squint in a Red-And-Green Macaw (*Ara chloropterus*) during slight head movement. (a) Pre-blink; (b) Upper lid falls and lower lid rises, causing them to come together; (c) Upper lid rises a little exposing the nictitating membrane; (d) Post-blink.

Videoing birds was not without its challenges. Stationary birds tended to preen themselves, obscuring the eyes, or to fall asleep. With birds with laterally situated eyes, usually only one eye could be seen at a time. This was not the case with the frontally oriented eyes of raptors. Nictitating membrane blinks were mainly associated with head movements and in small birds, such as finches (*Fringillidae*), honeyeaters (*Meliphagidae*) and fairywrens (*Maluridae*), these were so rapid that any blinking which might have occurred was often obscured by movement blur. It was sometimes hard to detect the movement of transparent nictitating membranes, particularly across a dark iris. This was the case in a number of species of the order Anseriformes. For the purposes of this study, no time limit was set on how long a blink could last, but for most species, blinks rarely lasted longer than a second or two, and most were much briefer.

3. Results

3.1. Birds

Video recordings were made on 591 bird species, which included 43 orders and 125 families (see Table A1). No blinking occurred during the period of observation (i.e., the bird flew away) in 67 species. Three types of blink were observed:

3.2. Nictitating Membrane Blinks

Here, the membrane travelled across the cornea from the inner (medial) to the outer (lateral) canthus (Figure 1).

Nictitating membrane blinks were usually frequent, rapid, brief and coincided with head movement. They also occurred with the head still. In the few species with preserved eye movements, nictitating membrane blinks also coincided with these (Figure 2).

Eye-movement-related nictitating membrane blinks were seen in Bucerotiformes and some species of Anseriformes, Ciconiiformes, Cuculiformes, Otidiformes, Passeriformes and Sphenisciformes. Eye movements were most noticeable in birds with large, long bills like hornbills (*Bucerotidae*), storks (*Ciconiidae*) and pelicans (*Pelecanidae*) but also in parrots (*Psittaciformes*) with large, short bills.

Nictitating membrane blinks were seen in the following orders: Accipitriformes, Anseriformes, Bucerotiformes, Cariamiformes, Casuariiformes, Cathartiformes, Ciconiiformes, Coraciiformes, Cuculiformes, Eurypygiformes, Falconiformes, Galliformes, Gruiformes, Musophagiformes, Otidiformes, Pelecaniformes, Phoenicopteriformes, Piciformes, Sphenisciformes, Suliformes and Tinamiformes.

In some species, the nictitating membrane blink was accompanied by a partial upper lid blink with slight lowering of the medial (nasal) side of the upper eyelid (Figure 3). In these species, the upper lid never covered the pupil. Partial upper lid blinks were seen in many species of Ciconiiformes, Galliformes and Pelecaniformes and a few species of Accipitriformes, Charadriiformes and Musophagiformes.

Birds with minimal eye movements, and even in those with easily observable eye movements, surveyed the landscape around them by frequent, rapid, brief head movements, akin to the saccadic (rapid, fixed velocity, voluntary) eye movements of humans [19]. Most, but not all, head movements were accompanied by nictitating membrane blinks.

Nictitating membrane blinks could be unilateral ('winks') or bilateral—asynchronous or synchronous. In larger species with less opaque membranes, arcades of blood vessels became visible during the course of a blink (Figure 4).

Nictitating membrane blinks were observed in 376 of 524 species which blinked (Table A1, and Table 1) and could not be seen in 91 species which had a blink of another sort (in some of these cases, the quality of the video was good enough to see eyelid movement but not nictitating membrane movement). In 70 species, the membrane was transparent. This was the case in 21/22 species of Anseriformes, 3/3 species of Phoenicopteriformes, 3/3 of the family Spheniscidae (order Sphenisciformes), 5/5 of Suliformes and in some species within Charadriiformes, Columbiformes, Galliformes, Pelecaniformes and Strigiformes. While most of the species with transparent nictitating membrane were

aquatic, there were many notable exceptions, including owls (Strigiformes). In 9/13 species of Bucerotiformes, nictitating membrane blinks were associated with eye movements.

Table 1. Number of species with each of the three types of blink and the total number of species videoed where a blink occurred.

Blink Type	Number of Species	Number Videoed
Nictitating membrane	376	524
Upper lid	166	524
Lower lid	77	524

More prolonged nictitating membrane blinks were associated with irregular rapid bobbing of the eye. This was described by Pettigrew [12] as saccadic oscillation. The shaking of the pecten, a highly vascular structure protruding into the vitreous humour, increases the release of oxygen and nutrients into the vitreous humour. These diffuse into the retina which, unlike the human eye, does not have its own blood supply [20]. Saccadic oscillation was seen most clearly in birds with large eyes such as the stone curlew. It was not seen with the naked eye—it requires 100 fps video capture.

3.3. Upper Eyelid Blinks

Here, there was downward (ventral) movement of the upper eyelid accompanied by horizontal movement of the nictitating membrane from the inner (medial) to outer (lateral) canthus (Figure 5), although the upper eyelid often obscured this (Figure 6).

As with ‘pure’ nictitating membrane blinks, upper lid blinks were usually rapid, brief and coincided with head movement. Occasionally, they were observed with the head still. The movements of the upper lid and nictitating membrane appeared to be linked during a blink, neither occurring alone, but their movements were not necessarily synchronous, one starting or finishing before or after the other.

Upper lid blinking was observed in 166 of 524 species which blinked (Table 1 and Table A1) and in 43 of these, accompanying movement of the nictitating membrane could be seen. Upper lid blinking was seen in 30/36 species of Columbiformes, in all 60 species of Psittaciformes, all 11 species of Caprimulgiformes and in 24/28 species of Strigiformes. In other orders, the proportion of upper blinks was lower: 7/40 species of Charadriiformes and 18/131 species of Passeriformes (8/14 of the family Estrildidae). In no case did a nictitating membrane blink occur without an accompanying upper lid blink in species displaying upper lid blinks.

In some species, the upper lid was made prominent by being a different colour from the rest of the head e.g., *Caloenas nicobarica* and *Momotus coeruliceps*, which have white upper lids.

3.4. Lower Eyelid Blinks

A total of 77 species (out of 524 species which blinked, Table 1 and Table A1) across most orders of bird were observed while preening (Figure 7) and 98 during drowsiness (Figure 8). These had lower lid blinks in which the lower lid rose, usually slowly and in a sustained manner. Before sleep, the lower lid would rise and fall repeatedly, before eventually remaining elevated. Often, the nictitating membrane could be seen making a pass as the lower lid rose (Figure 9), but it did not usually stay out for the entire duration of the lower lid blink, unlike upper lid blinks.

The lower lid in some species (e.g., *Radjah radjah*, *Columba guinea*) was paper thin, presumably allowing some light to enter the pupil. In others it was of a different colour to the rest of the head, making it prominent (e.g., *Hypotaenidia philippensis*). Rarely, species used the nictitating membrane rather than the lower lid during preening (e.g., *Scopus umbretta*).

In addition to the three types of blink, two further behaviours involving blinking were noted:

3.5. Pecking

Domestic hens (*Gallus gallus domesticus*) were observed pecking lichen off an old corrugated-iron panel. Their bills had been worn down. What was noticeable was that with every peck, a nictitating membrane blink occurred as the bill reached a certain distance from the target. In pigeons (Columbiformes), each peck was accompanied by an upper and lower lid blink (Figure 10). The type of blink seen with pecking varied with the species:

Lower lid blink on pecking: *Numenius madagascariensis*, *Alectoris chukar*, *Phasianus colchicus*, *Colinus virginianus*, *Nymphicus hollandicus*.

Upper lid blink on pecking: *Turnix melanogaster*, *Geopelia cuneata*, *Geopelia striata*, *Ocyphaps lophotes*, *Spilopelia chinensis*, *Spilopelia senegalensis*, *Streptopelia risorii*, *Nymphicus hollandicus*.

Upper and lower lids involved in pecking: *Pluvialis fulva*, *Columba livia domestica*, *Columba palumbus*, *Coturnix japonica*, *Taeniopygia guttata*, *Barnardius zonarius*, *Platycercus eximius*, *Psephotus haematonotus*.

3.6. Synergic Upper and Lower Eyelid Moment

A curious phenomenon seen mainly in Columbiformes, Psittaciformes and Strigiformes in states of drowsiness involved the upper lid slowly descending until it reached the lower lid in its resting position. The lower lid would then slowly rise, the upper lid rising at the same pace so that the eye remained closed. The two lids would then rise and fall together in unison, until the eye eventually opened (Figure 11).

Sometimes, the bird would squint, the lids coming together leaving a small gap or slit through which the pupil could be seen (Figures 12–14)

Sometimes, the nictitating membrane was visible during a squint (Figure 15).

3.7. Crocodilia

Videos were made of 15 species of Crocodilia from 3 families (Table A2). This was a more time-consuming exercise than with birds, as many minutes could pass between blinks. Nictitating membrane blinks were seen in 15 species, 3 with visible globe retraction, 4 with no evident globe retraction (Figure 16) and 11 associated with globe retraction and elevation of the lower lid (Figure 17). In five species, there was lower lid elevation and globe retraction without visible movement of the nictitating membrane. In no case was there upper lid blinking, though in some cases the upper lid sank a little into the orbit as the globe retracted.

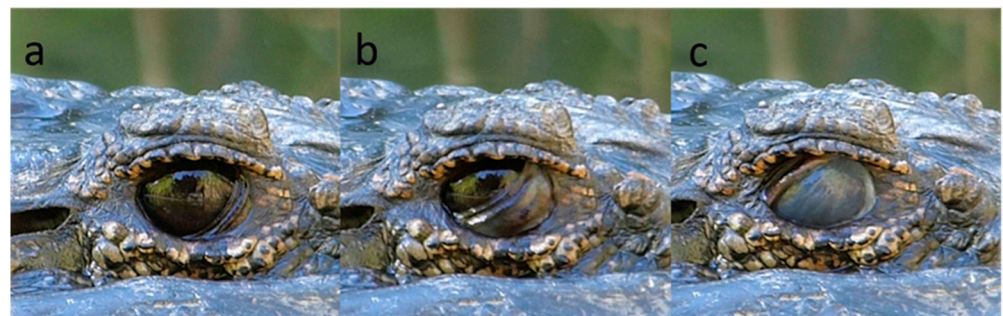


Figure 16. Nictitating membrane blink in an American Alligator (*Alligator mississippiensis*). Sequence: (a): pre-blink, edge of nictitating membrane visible at inner fornix; (b): nictitating membrane half covers the cornea; (c): nictitating membrane covers the cornea. No change in diameter of palpebral fissure, so no evidence of globe retraction.

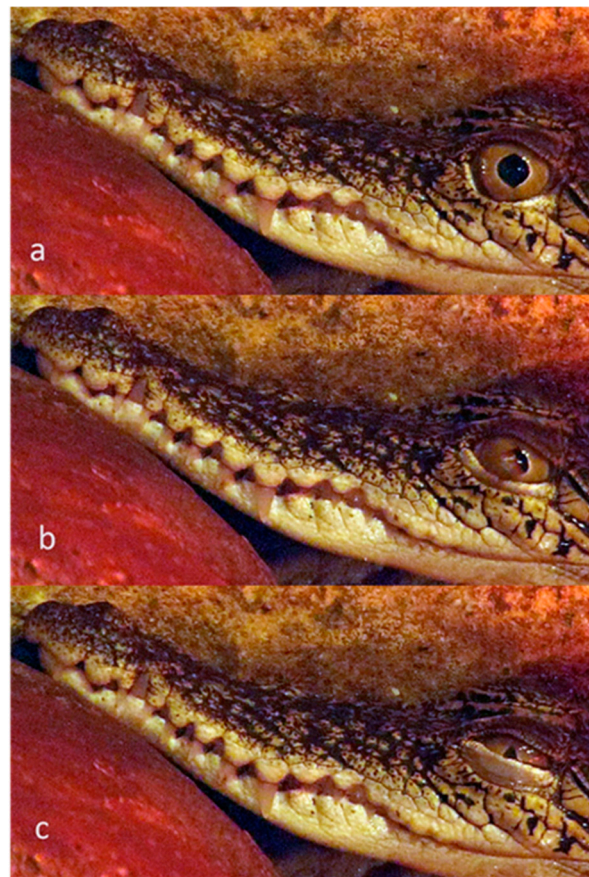


Figure 17. Nictitating membrane and lower lid blink in a drowsy juvenile Saltwater Crocodile (*Crocodylus porosus*). Sequence: (a): pre-blink; (b): nictitating membrane half covers the pupil and lower lid starts to rise; (c): lower lid half elevated.

4. Discussion

The present study confirms the observation of Curio [18] that blinking in birds appears to be of two types, phasic and tonic.

Phasic blinks were frequent, rapid and brief and involved the nictitating membrane and, in some species, the upper lid as well. They occurred during head movement associated with a shift in gaze [16]. Not every shift in gaze was accompanied by a blink, and some blinks, even flurries of blinks, were observed with the head still. Phasic blinks spread tears from the Harderian gland over the surface of the cornea. Debris on the surface of the cornea is also swept towards the medial canthus. Tear fluid drains into puncti on the inner end of the upper and lower eyelid and into the lacrimal duct, and thence to the anterior/cranial nasal cavity.

Tonic blinks were infrequent, slow and sustained, occurring with drowsiness and during preening and involving the nictitating membrane and lower lid. They appear to have the function of protecting the eye from feathers and ‘feather dust’ during preening (and from the bill of other birds preening them). The lower lid would rise and fall as a prelude to sleep and then remain raised during sleep. This protects the eye from exposure and foreign material and shuts out light. That said, it was not uncommon to find that the lower eyelids were paper thin when closed. Tonic blinks are likely to be less effective than phasic blinks in distributing tear fluid and removing debris as they occur less frequently.

During prolonged blinks and during sleep, the cornea is no longer exposed to atmospheric oxygen. In humans, gas exchange continues during sleep by virtue of the rich supply of capillaries on the conjunctival side of the eyelids [21]. If these are also present in birds, gas exchange might be impaired when the nictitating membrane comes between

the cornea and the eyelids. It may be significant therefore that the nictitating membrane appears to have a rich arcade of blood vessels.

Involvement of the lower lid in tonic blinks is seen in frogs, turtles, lizards (personal observations), crocodiles as well as birds. This may hark back to the time when fish leaving the sea adopted an amphibious lifestyle. Half-submerged in water, elevation of the lower lid protects the eye from floating debris. In crocodiles, a ‘submergence reflex’, where the lower eyelid elevates and the external auditory meatus closes as the water level rises, has been described [22].

Of particular interest is the finding that in some orders and families of birds, phasic blinks involve not only the nictitating membrane but also the upper lid. It is likely that this feature evolved after the emergence of nictitating membrane blinks, as Crocodilia only blink with their nictitating membranes and lower lids. With birds, Crocodilia are the only living descendants of archosaurs, a group of diapsid amniotes which once included dinosaurs and pterosaurs. While birds have evolved over the last 165–150 million years into 10,000 or so extant species ranging greatly in size, shape and habitat [23], Crocodilia have evolved into only 23 extant species and have changed little since they first appeared [24]. Upper lid blinks were not found in Paleognathae (ratites and tinamous) or Galloanserae (land fowl and waterfowl), only in the Neoaves clade which underwent a rapid expansion following the Cretaceous–Paleogene mass extinction [25].

Upper eyelid blinks were seen mainly in four orders: Columbiformes, Strigiformes, Psittaciformes and Caprimulgiformes. The question arises, what were the factors which led to this? Have they perhaps evolved from a common ancestor which blinked with its upper eyelids? According to a recent genomic analysis of clade genotypes [25], these four orders are not closely related (Table A3). Columbiformes are classified within Columbaves which includes turacos, which do not blink with their upper eyelids. Strigiformes lie between Accipitriformes and Coraciiformes, neither of which blink with their upper eyelids. Psittaciformes are classed with Australaves, a group which includes falcons, which do not blink with their upper eyelids. Caprimulgiformes is an order which includes swifts and hummingbirds. In short, no clear pattern of genetic association emerges. Further evidence that upper lid blinking is not related to clade genotypes comes from the finding that even within orders such as Passeriformes and Charadriiformes, which mostly blink with their nictitating membranes, there were families which blinked with their upper lids.

No clear association was apparent between upper lid blinking and nocturnality. Of the orders with upper lid blinks, Strigiformes is the only one which is almost exclusively nocturnal (the exceptions being the northern hawk-owl, *Surnia ulula*, and the burrowing owl, *Athene cunicularia*). Within the order of Caprimulgiformes, nightjars (Caprimulgidae) are nocturnal but swifts (Apodidae) and hummingbirds (Trochilidae) are not. Columbiformes and Psittaciformes are diurnal.

These findings suggest that upper lid blinking is the result of convergent evolution. So, what might have been the factors which favoured upper lid blinking? Movement of objects in air tends to be of a higher velocity than in water and therefore more potentially injurious. Birds cannot retract their eyes, and it is retraction in other classes of animal which provides the most protection from blunt mechanical injury [26]. While the lower lid can cover the eye, it tends to move slowly. The rapidly moving upper lids and nictitating membranes might provide reflex closure of the eyes in response to a visual threat (menace reflex) [27], touching of the feather-equivalent of eyelashes by potentially damaging objects like twigs or leaves (lash response) [28] or touching the cornea (corneal reflex) [7].

This begs the question, are birds which blink with their upper lids at greater risk of eye injury than other birds? This may be the case in ground-feeding birds like pigeons (Columbidae) and quails (Phasianidae) which peck for seeds in undergrowth and foliage. A common finding was of blinking with every peck but this could involve the nictitating membrane, upper lid, lower lid or both, depending on the species. Protection during blinking does not depend on having a mobile upper lid. In the case of owls and nightjars, catching live prey capable of injuring their eyes at night may put them at greater risk

than other raptors which hunt during the day when visibility is better. But the lower lid and nictitating membrane could also provide this protection. A paper by Ostheim and colleagues [29] raised another possibility. The amount of light focused on the retina by the cornea and lens is related to the size of the pupil. Ostheim and colleagues [29] showed that, in the case of pigeons, the eyelids may also play a role under certain conditions. They found that during pecking, pigeons do not close their eyes completely. The effect of this is to turn the round aperture of the pupil into a narrow horizontal slit, thereby increasing the depth of field [30]. This would result in sharper retinal images of the target, even at close range. For this to occur, upper and lower lids need to come together synergistically. Such behaviour was observed in pigeons, parrots and owls, albeit with drowsiness.

It is hard to know what to make of the many species of bird with partial upper lid blinks—where the inner part of the upper lid lowered a little during a nictitating membrane blink. It did not appear to be produced by eye movement. Perhaps, in these species, upper lid blinks are in the process of evolving into existence—or perhaps out of existence?

Birds and crocodilians both blink with their nictitating membranes to lubricate and clear debris from the cornea. Crocodilia and aquatic birds, such as cormorants (Phalacrocoracidae), may protect their eyes while submerged without losing all vision, using their nictitating membranes, though this has not been established. Certainly, there is a preponderance of transparent nictitating membranes in birds which forage aquatically. Under water, the cornea and nictitating membrane contribute little to refraction of light entering the eye as the cornea is thin and the refractive indices of water and aqueous humour in the anterior chamber of the eye are similar [31]. Birds protect their eyes during sleep and preening by raising the lower eyelids, which are often quite flimsy. By contrast, Crocodilia protect their eyes from injury by retracting the eyeballs deep into the orbits. In saltwater crocodiles, this causes the thickly armored, hinged, upper eyelids to fold like a trapdoor to cover over the orbits. The lower eyelids are also raised. Having larger prey than birds, the requirements of Crocodilia for protection of the eyes are likely to be more stringent than is the case for most birds. In the evolutionary balancing act of reducing body weight while increasing visual acuity, birds have mostly abandoned extraocular muscles which move the eyes and retract them, while increasing the size of the eyes relative to their body mass.

5. Conclusions

Birds (and Crocodilia) have two types of blink: rapid brief (phasic) nictitating membrane blinks; and slow sustained (tonic) lower eyelid blinks. In some avian orders, and in some families within others, phasic nictitating membrane blinks are accompanied by upper eyelid blinks.

Phasic blinks occur on head turn and pecking, tonic blinks on preening and with drowsiness. Nocturnality does not particularly predispose to any blink type.

Upper lid blinking cannot readily be related to phylogeny. The orders where it occurs in every species are not closely related. This type of blinking is probably the result of convergent evolution.

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Appendix A

Table A1. Upper lid blinks in avian species, F: number of species within a family; S: number of species studied; A/B: A our video/B internet video; FUL: full upper lid blink; Y: yes; “_”: not seen; PUL: partial upper lid blink.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
Accipitriformes	Accipitridae	<i>Accipiter novaehollandiae</i>	Grey goshawk	249	28	A		Y
		<i>Aquila audax</i>	Wedge-tailed eagle			A		
		<i>Aquila rapax</i>	Tawny eagle			A		
		<i>Aviceda subcristata</i>	Pacific baza			A		
		<i>Buteo buteo</i>	Common buzzard			A		
		<i>Buteo rufofuscus</i>	Jackal buzzard			A		
		<i>Buteo trizonatus</i>	Forest buzzard			A		
		<i>Elanus coeruleus</i>	Black-winged kite			A		
		<i>Gypohierax angolensis</i>	Palm-nut vulture			A		
		<i>Gyps africanus</i>	White-backed vulture			A		
		<i>Gyps fulvus</i>	Griffon vulture			A		
		<i>Haliaeetus leucocephalus</i>	Bald eagle			A		
		<i>Haliaeetus leucogaster</i>	White-bellied sea eagle			A		
		<i>Haliastur indus</i>	Brahminy kite			A		Y
		<i>Haliastur sphenurus</i>	Whistling kite			A		Y
		<i>Hamirostra melanosternon</i>	Black-breasted buzzard			A		
		<i>Hieraaetus morphnoides</i>	Little eagle			A		
		<i>Hieraaetus wahlbergi</i>	Wahlberg's eagle			A		
		<i>Hieraaetus morphnoides</i>	Little eagle			A		
		<i>Ictinaetus malaiensis</i>	Black eagle			A		
		<i>Melierax canorus</i>	Pale chanting goshawk			A		
		<i>Milvus migrans</i>	Black kite			A		
		<i>Nisaetus nanus</i>	Wallace's hawk-eagle			A		
		<i>Parabuteo unicinctus</i>	Harris' hawk			A		
		<i>Polyboroides typus</i>	African harrier hawk			A		
		<i>Polemaetus bellicosus</i>	Martial eagle			A		
		<i>Stephanoaetus coronatus</i>	Crowned eagle			A		
		<i>Terathopius ecaudatus</i>	Bateleur			A		
		<i>Trionoceph occipitalis</i>	White-headed vulture			A		
	Sagittariidae	<i>Sagittarius serpentarius</i>	Secretary bird	1	1	A		

Table A1. Cont.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
Cathartiformes	Cathartidae	<i>Gymnogyps californianus</i>	California condor	7	5	A		
		<i>Cathartes aura</i>	Turkey vulture			A		Y
		<i>Vultur gryphus</i>	Andean condor			A		
		<i>Coragyps atratus</i>	Black vulture			A		
		<i>Sarcoramphus papa</i>	King vulture			A		
	Pandionidae	<i>Pandion haliaetus</i>	Western osprey	1	1	A		Y
Anseriformes	Anatidae	<i>Aix galericulata</i>	Mandarin duck	174	48	A		
		<i>Aix sponsa</i>	Wood duck			A		Y
		<i>Alopochen aegyptiaca</i>	Egyptian goose			A		
		<i>Anas castanea</i>	Chestnut teal			A		
		<i>Anas georgica</i>	Yellow-billed pintail			A		–
		<i>Anas platyrhynchos</i>	Mallard			A		
		<i>Anas superciliosa</i>	Pacific black duck			A		
		<i>Anas undulata</i>	Yellow-billed duck			A		
		<i>Anser anser</i>	Graylag goose			A		
		<i>Anser cygnoides</i>	Swan goose			A		–
		<i>Anser indicus</i>	Bar-headed goose			A		–
		<i>Asarcornis scutulata</i>	White-winged duck			A		–
		<i>Aythya affinis</i>	Lesser scaup			A		–
		<i>Aythya australis</i>	Hardhead			A		
		<i>Aythya fuligula</i>	Tufted duck			A		
		<i>Aythya nyroca</i>	Ferruginous duck			A		–
		<i>Aythya valisineria</i>	Canvasback			A		–
		<i>Branta canadensis</i>	Canada goose			A		
		<i>Branta leucopsis</i>	Barnacle goose			A		–
		<i>Branta sandvicensis</i>	Nene			A		–
		<i>Bucephala albeola</i>	Bufflehead			A		–
		<i>Cairina moschata</i>	Muscovy duck			A		
		<i>Callonetta leucophrys</i>	Ringed teal			A		
		<i>Cereopsis novaehollandiae</i>	Cape Barren goose			A		
		<i>Chenonetta jubata</i>	Australian wood duck			A		
		<i>Cygnus atratus</i>	Black swan			A		
		<i>Cygnus cygnus</i>	Whooper swan			A		
		<i>Cygnus olor</i>	Mute swan			A		–
		<i>Dendrocygna arcuata</i>	Wandering whistling duck			A		
		<i>Dendrocygna bicolor</i>	Fulvous whistling duck			A		Y
		<i>Dendrocygna eytoni</i>	Plumed whistling duck			A		–
		<i>Dendrocygna viduata</i>	White-faced whistling duck			A		–

Table A1. Cont.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
		<i>Lophodytes cucullatus</i>	Hooded merganser			A		–
		<i>Hymenolaimus malacorhynchos</i>	Blue duck or whio			A		
		<i>Mergellus albellus</i>	Smew			A		–
		<i>Mergus merganser</i>	Common merganser			A		
		<i>Mergus serrator</i>	Red-breasted merganser			A		–
		<i>Neochen jubata</i>	Orinoco goose			A		–
		<i>Nettapus auritus</i>	African pygmy goose			A		
		<i>Netta rufina</i>	Red-crested pochard			A		
		<i>Oxyura australis</i>	Blue-billed duck			A		
		<i>Radjah radjah</i>	Radjah shelduck			A		
		<i>Sarkidiornis sylvicola</i>	Comb duck			A		–
		<i>Somateria fischeri</i>	Spectacled eider			A		Y
		<i>Somateria mollissima</i>	Common eider			A		–
		<i>Spatula hottentota</i>	Hottentot teal			A		
		<i>Tadorna ferruginea</i>	Ruddy shelduck			A		
		<i>Tadorna variegata</i>	Paradise shelduck			A		–
	Anseranatidae	<i>Anseranas semipalmata</i>	Magpie goose	1	1	A		
	Anhimidae	<i>Chauna torquata</i>	Southern screamer	3	1	A		
Apterygiformes	Apterygidae	<i>Apteryx australis</i>	Kiwi	5	1	B		–
Bucerotiformes	Bucerotidae	<i>Berenicornis comatus</i>	White-crowned hornbill	59	11	A		
		<i>Buceros bicornis</i>	Great hornbill			A		
		<i>Buceros hydrocorax</i>	Rufous hornbill			A		
		<i>Buceros rhinoceros</i>	Rhinoceros hornbill			A		
		<i>Bycanistes brevis</i>	Silvery-cheeked hornbill			A		
		<i>Horizocerus albocristatus</i>	White-crested hornbill			A		
		<i>Lophoceros fasciatus</i>	African pied hornbill			A		
		<i>Lophoceros nasutus</i>	African grey hornbill			A		
		<i>Rhyticeros plicatus</i>	Blyth's (Papuan) hornbill			A		
		<i>Rhyticeros undulatus</i>	Wreathed hornbill			A		
		<i>Tockus deckeni</i>	Von der Decken's hornbill			A		
	Bucorvidae	<i>Bucorvus leadbeateri</i>	Southern ground hornbill	2	2	A		
		<i>Rhabdotorrhinus exarhatus</i>	Sulawesi hornbill			A		
	Upupidae	<i>Upupa epops</i>	Eurasian hoopoe	2	1	A/B		
	Phoeniculidae	<i>Phoeniculus purpureus</i>	Green wood hoopoe	8	1	A/B		

Table A1. Cont.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
Caprimulgiformes	Aegothelidae	<i>Aegotheles cristatus</i>	Australian owl nightjar	9	1	B	Y	
	Apodidae	<i>Aeronautes saxatalis</i>	White-throated swift	12	2	B	Y	
		<i>Apus apus</i>	Common swift			B	Y	
	Hemiprocidae	<i>Hemiprocne comata</i>	Whiskered treeswift	4	1	B	Y	
	Caprimulgidae	<i>Caprimulgus europaeus</i>	European nightjar	96	2	B	Y	
		<i>Lyncornis macrotis</i>	Great eared nightjar			B	Y	
	Nyctibiidae	<i>Nyctibius grandis</i>	Great potoo	7	1	B	Y	
	Trochilidae	<i>Calypte anna</i>	Anna's hummingbird	363	4	B	Y	
		<i>Calypte costae</i>	Costa's hummingbird			B	Y	
		<i>Mellisuga helenae</i>	Bee hummingbird			B	Y	
		<i>Selasphorus sasin</i>	Allen's hummingbird			B	Y	
Cariamiformes	Cariamidae	<i>Cariama cristata</i>	Red-legged seriema	2	1	A		
Casuariiformes	Casuariidae	<i>Dromaius novaehollandiae</i>	Emu	4	2	A		
		<i>Casuaris casuarius</i>	Southern cassowary			A		
Charadriiformes	Turnicidae	<i>Turnix castanotus</i>	Chestnut-backed buttonquail	18	3	A/B	Y	
		<i>Turnix melanogaster</i>	Black-breasted buttonquail			A	Y	
		<i>Turnix varius</i>	Painted buttonquail			A	Y	
	Haematopodidae	<i>Haematopus fuliginosus</i>	Sooty oystercatcher	12	4	A	–	
		<i>Haematopus longirostris</i>	Pied oystercatcher			A		
		<i>Haematopus moquini</i>	African oyster catcher			A	–	
		<i>Haematopus ostralegus</i>	Eurasian oystercatcher			A		
	Burhinidae	<i>Burhinus capensis</i>	Spotted thick-knee	10	3	A/B		Y
		<i>Burhinus grallarius</i>	Bush stone-curlew			A		Y
		<i>Esacus magnirostris</i>	Beach stone-curlew			A		Y
	Laridae	<i>Chroicocephalus hartlaubii</i>	Hartlaub's gull	99	14	A/B		
		<i>Chroicocephalus novaehollandiae</i>	Silver gull			A/B		Y
		<i>Chroicocephalus ridibundus</i>	Black-headed gull			A/B		
		<i>Rissa tridactyla</i>	Black-legged kittiwake			A/B		Y
		<i>Gygis alba</i>	White tern			A/B		–
		<i>Hydroprogne caspia</i>	Caspian tern			B		–
		<i>Larosterna inca</i>	Inca tern			A		
		<i>Larus argentatus</i>	European herring gull			A		
		<i>Larus marinus</i>	Great black-backed gull			A		

Table A1. Cont.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
		<i>Larus pacificus</i>	Pacific gull			A/B		
		<i>Larus dominicanus</i>	Kelp gull			A		
		<i>Rhinchops niger</i>	Black skimmer			B		
		<i>Sterna striata</i>	White-fronted tern			A		–
		<i>Thalasseus bergii</i>	Greater crested tern			A		
	Scolopacidae	<i>Numenius madagascariensis</i>	Far Eastern curlew	97	4	A/B		–
		<i>Tringa nebularia</i>	Common greenshank			A	Y	
		<i>Calidris canutus</i>	Red knot			A/B	Y	
		<i>Tringa totanus</i>	Common redshank			A	Y	
	Recurvirostridae	<i>Himantopus himantopus</i>	Black-winged stilt	9	3	A		Y
		<i>Recurvirostra avosetta</i>	Pied avocet			A	Y	
		<i>Recurvirostra novaehollandiae</i>	Red-necked avocet			A	Y	
	Alcidae	<i>Fratercula cirrhata</i>	Tufted puffin	25	2	A	Y	Y
		<i>Uria aalge</i>	Common guillemot			A		Y
	Charadriidae	<i>Charadrius mongolus</i>	Lesser sand plover	68	7	A/B		Y
		<i>Elsya melanops</i>	Black-fronted dotterel			A/B		–
		<i>Vanellus miles</i>	Masked lapwing			A		Y
		<i>Vanellus spinosus</i>	Spur-winged lapwing			A		–
		<i>Vanellus tricolor</i>	Banded lapwing			A		Y
		<i>Pluvialis fulva</i>	Pacific golden plover			A		Y
		<i>Thinornis cucullatus</i>	Hooded plover			A		–
	Jacaniidae	<i>Irediparra gallinacea</i>	Comb-crested jacana	8	1	A		Y
Ciconiiformes	Ciconiidae	<i>Ciconia stormi</i>	Storm's stork	20	12	A		Y
		<i>Ciconia abdimii</i>	Abdim's stork			A		Y
		<i>Ciconia ciconia</i>	White stork			A		Y
		<i>Ciconia episcopus</i>	Woolly-necked stork			A		Y
		<i>Ciconia nigra</i>	Black stork			A		Y
		<i>Ciconia stormi</i>	Storm's stork			A		Y
		<i>Ephippiorhynchus asiaticus</i>	Black-necked stork			A		Y
		<i>Ephippiorhynchus senegalensis</i>	Saddle-billed stork			A		Y
		<i>Leptoptilos crumenifer</i>	Marabou stork			A		Y
		<i>Mycteria cinerea</i>	Milky stork			A		Y
		<i>Mycteria leucocephala</i>	Painted stork			A		Y
		<i>Mycteria ibis</i>	Yellow-billed stork			A		Y
Coliiformes	Coliidae	<i>Colius colius</i>	White-backed mousebird	6	2	B		Y
		<i>Uroclius indicus</i>	Red-faced mousebird			B		Y

Table A1. Cont.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
Columbiformes	Columbidae	<i>Caloenas nicobarica</i>	Nicobar pigeon	353	37	A	Y	
		<i>Chalcophaps indica</i>	Common emerald dove			A	Y	
		<i>Columba arquatrix</i>	African olive pigeon			A	Y	
		<i>Columba guinea</i>	Speckled pigeon			A	Y	
		<i>Columba leucomela</i>	White-headed pigeon			A	Y	
		<i>Columba livia domestica</i>	Domestic pigeon			A	Y	
		<i>Columba palumbus</i>	Common wood pigeon			A	Y	
		<i>Ducula aenea</i>	Green imperial pigeon			A	Y	
		<i>Ducula bicolor</i>	Pied imperial pigeon			A	Y	
		<i>Ducula spilorrhoa</i>	Torresian imperial pigeon			A	Y	
		<i>Gallicolumba crinigera</i>	Mindanao bleeding-heart			A/B	Y	
		<i>Gallicolumba tristigmata bimaculata</i>	Sulawesi ground dove			A	Y	
		<i>Geopelia cuneata</i>	Diamond dove			A	Y	
		<i>Geopelia humeralis</i>	Bar-shouldered dove			A	Y	
		<i>Geopelia striata</i>	Zebra dove			A	Y	
		<i>Geophaps plumifera</i>	Spinifex pigeon			A	Y	
		<i>Geophaps scripta</i>	Squatter pigeon			A	Y	
		<i>Genus macropygia</i>	Cuckoo dove			A	Y	
		<i>Goura victoria</i>	Victoria crowned pigeon			A	Y	
		<i>Hemiphaga novaeseelandiae</i>	Kererū			A	Y	
		<i>Leucosarcia melanoleuca</i>	Wonga pigeon			A	Y	
		<i>Lopholaimus antarcticus</i>	Topknot pigeon			A	Y	
		<i>Macropygia phasianella</i>	Brown cuckoo-dove			A	Y	
		<i>Ocyphaps lophotes</i>	Crested pigeon			A	Y	
		<i>Otidiphaps nobilis</i>	Pheasant pigeon			A/B	Y	
		<i>Pampusana jobiensis</i>	White-bibbed ground dove			A	Y	
		<i>Phaps elegans</i>	Brush bronzewing			A	Y	
		<i>Phaps histrionica</i>	Flock bronzewing			A/B	Y	
		<i>Ptilinopus magnificus</i>	Wompoo fruit dove			A	Y	
		<i>Ptilinopus regina</i>	Rose-crowned fruit dove			A	Y	
		<i>Ptilinopus superbus</i>	Superb fruit dove			A	Y	
		<i>Streptopelia decipiens</i>	African mourning dove			A	Y	
		<i>Spilopelia chinensis</i>	Spotted dove			A/B	Y	

Table A1. Cont.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
Coraciiformes	Meropidae	<i>Spilopelia senegalensis</i>	Laughing dove			A/B	Y	
		<i>Streptopelia risoria</i>	Barbary dove			A	Y	
		<i>Zenaida macroura</i>	Mourning dove			A	Y	
		<i>Merops albicollis</i>	White-throated bee-eater	31	4	A		
		<i>Merops bullockoides</i>	White-fronted bee-eater			A		
		<i>Merops nubicus</i>	Northern carmine bee-eater			A/B		
		<i>Merops ornatus</i>	Rainbow bee-eater			A/B		
	Alcedinidae	<i>Dacelo leachii</i>	Blue-winged kookaburra	117	7	A		
		<i>Dacelo novaeguineae</i>	Laughing kookaburra			A		
		<i>Halcyon coromanda</i>	Ruddy kingfisher			A		
		<i>Todiramphus chloris</i>	Collared kingfisher			A		
		<i>Todiramphus cinnamominus</i>	Guam kingfisher			A		
		<i>Todiramphus macleayii</i>	Forest kingfisher			A		
		<i>Todiramphus sanctus</i>	Sacred kingfisher			A		
	Coraciidae	<i>Coracias cyanogaster</i>	Blue-bellied roller	13	2	A		
		<i>Eurystomus orientalis</i>	Oriental dollarbird			A		
Cuculiformes	Cuculidae	<i>Cuculus canoris</i>	Common cuckoo	147	9	B		
		<i>Centropus phasianinus</i>	Pheasant coucal			A		
		<i>Centropus sinensis</i>	Greater coucal			B		
		<i>Crotophaga major</i>	Greater ani			B		
		<i>Dromococcyx pavoninus</i>	Pavonine cuckoo			B		
		<i>Dromococcyx phasianellus</i>	Pheasant cuckoo			B		
		<i>Guira guira</i>	Guira cuckoo			A		
		<i>Morococcyx erythropygus</i>	Lesser ground-cuckoo			B		
		<i>Scythrops novaehollandiae</i>	Channel-billed cuckoo			A		
Eurypygiiformes	Eurypygidae	<i>Eurypyga helias</i>	Sunbittern	1	1	A/B		
	Rhinichetidae	<i>Rhinichetus jubatus</i>	Kagu	1	0	B	—	
Falconiformes	Falconidae	<i>Caracara plancus</i>	Crested caracara	65	7	A/B		
		<i>Falco cenchroides</i>	Nankeen kestrel			A		
		<i>Falco columbarius</i>	Merlin			A/B		
		<i>Falco rupicolus</i>	Rock kestrel			A		
		<i>Falco subbuteo</i>	Eurasian hobby			A		
		<i>Phalcoboenus australis</i>	Striated caracara			A		
		<i>Phalcoboenus megalopterus</i>	Mountain caracara			A		

Table A1. Cont.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
Galbuliformes	Bucconidae	<i>Malacoptila fusca</i>	White-chested Puffbird	37	1	B		
	Galbulidae	<i>Galbula ruficauda</i>	Rufus tailed jacamar	18	1	B		
Galliformes	Cracidae	<i>Pauxi pauxi</i>	Helmeted curassow	57	2	A		
		<i>Nothocrax urumutum</i>	Nocturnal curassow			A		
	Numididae	<i>Acryllium vulturinum</i>	Vulturine guineafowl	8	2	A		
		<i>Numida meleagris</i>	Helmeted guineafowl			A		
	Phasianidae	<i>Afropavo congensis</i>	Congo peafowl	186	22	A		Y
		<i>Arborophila atrogularis</i>	White-cheeked partridge			A/B		Y
		<i>Alectoris chukar</i>	Chukar partridge			A		
		<i>Argusianus argus</i>	Great argus			A		
		<i>Chrysolophus amherstiae</i>	Lady Amherst's pheasant			A		
		<i>Chrysolophus pictus</i>	Golden pheasant			A		
		<i>Coturnix japonica</i>	Japanese quail			A/B		Y
		<i>Gallus gallus domesticus</i>	Chicken			A		Y
		genus <i>Meleagris</i>	Turkey			A		
		<i>Lophophorus impejanus</i>	Himalayan monal			A		Y
		<i>Lophura bulweri</i>	Bulwer's pheasant			A/B		
		<i>Lophura diardi</i>	Siamese fireback			A		Y
		<i>Lophura nycthemera</i>	Silver pheasant			A		
		<i>Pavo cristatus</i>	Indian peafowl			A		Y
		<i>Pavo muticus</i>	Green peafowl			A		
		<i>Phasianus colchicus</i>	Common pheasant			A		Y
		<i>Polyplectron inopinatum</i>	Mountain peacock-pheasant			A		Y
		<i>Polyplectron napoleonis</i>	Palawan peacock-pheasant			A		
		<i>Rollulus rouloul</i>	Crested partridge			A/B		
		<i>Synoicus chinensis</i>	King quail			A		Y
		<i>Synoicus ypsilophorus</i>	Brown quail			A		Y
		<i>Tragopan temminckii</i>	Temminck's tragopan			A		
	Odontophoridae	<i>Colinus virginianus</i>	Northern bobwhite	33	2	A		Y
		<i>Ptilopachus petrosus</i>	Stone partridge			A/B		Y
	Megapodiidae	<i>Alectura lathamii</i>	Australian brushturkey	21	3	A		
		<i>Leipoa ocellata</i>	Malleefowl			A		
		<i>Megapodius reinwardt</i>	Orange-footed scrubfowl			A		Y
Gaviiformes	Gaviidae	<i>Gavia immer</i>	Common loon	5	1	B		
Gruiformes	Gruidae	<i>Antigone rubicunda</i>	Brolga	15	5	A		

Table A1. Cont.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
		<i>Antigone vipio</i>	White-naped crane			A		
		<i>Balearica regulorum</i>	Grey-crowned crane			A		
		<i>Grus japonensis</i>	Red-crowned crane			A		Y
		<i>Grus paradisea</i>	Blue crane			A		
	Psophiidae	<i>Psophia crepitans</i>	Grey-winged trumpeter	3	1	A		
	Rallidae	<i>Eulabeornis castaneiventris</i>	Chestnut rail	159	8	A/B		
		<i>Fulica atra</i>	Eurasian coot			A		
		<i>Gallinula tenebrosa</i>	Dusky moorhen			A		
		<i>Hypotaenidia philippensis</i>	Buff-banded rail			A		
		<i>Porphyrio hochstetteri</i>	Takahē			A		
		<i>Porphyrio melanotus</i>	Australasian swamphe			A		
		<i>Tribonyx mortierii</i>	Tasmanian nativehen			A		
		<i>Tribonyx ventralis</i>	Black-tailed nativehen			A		
Leptosomiformes	Leptosomidae	<i>Leptosomus discolor</i>	Cuckoo roller	1	1	B		
Mesitornithiformes	Mesitornithidae	<i>Monias benschi</i>	Subdesert mesite	3	1	B		
Musophagiformes	Musophagidae	<i>Crinifer piscator</i>	Western plantain-eater	23	6	A		
		<i>Tauraco erythrolophus</i>	Red-crested turaco			A		
		<i>Tauraco rossae</i>	Lady Ross's turaco			A		Y
		<i>Menelikornis leucotis</i>	White-cheeked turaco			A		
		<i>Tauraco persa</i>	Guinea turaco			A		
		<i>Tauraco violaceus</i>	Violet turaco			A		Y
Opisthocomiformes	Opisthocomidae	<i>Opisthocomus hoazin</i>	Hoatzin	1	1	B		
Otidiformes	Otididae	<i>Ardeotis australis</i>	Australian bustard	26	1	A		Y
Passeriformes	Acanthizidae	<i>Sericornis frontalis</i>	White-browed scrubwren	66	2	A		–
		<i>Acanthiza pusilla</i>	Brown thornbill			A		
	Acrocephalidae	<i>Acrocephalus australis</i>	Australian reed warbler	59	1	A		–
	Artamidae	<i>Alauda arvensis</i>	Eurasian skylark	24	10	A		Y
		<i>Artamus cyanopterus</i>	Dusky woodswallow			A		–
		<i>Artamus leucorhynchus</i>	White-breasted woodswallow			A		
		<i>Artamus superciliosus</i>	White-browed woodswallow			A		
		<i>Cracticus nigrogularis</i>	Pied butcherbird			A		Y
		<i>Cracticus torquatus</i>	Grey butcherbird			A		
		<i>Melloria quoyi</i>	Black butcherbird			A		
		<i>Gymnorhina tibicen</i>	Australian magpie			A		
		<i>Strepera graculina</i>	Pied currawong			A		
		<i>Strepera versicolor</i>	Grey currawong			A/B		
	Callaeidae	<i>Callaeas wilsoni</i>	North Island kōkako	5	1	B		

Table A1. Cont.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
	Campephagidae	<i>Coracina novaehollandiae</i>	Black-faced cuckooshrike	89	2	A		Y
		<i>Coracina papuensis</i>	White-bellied cuckooshrike			A		
	Cisticolidae	<i>Cisticola exilis</i>	Golden-headed cisticola	162	1	A/B		
	Corcoracidae	Genus <i>Corcoracidae</i>	White-winged chough	2	2	B		
		<i>Struthidea cinerea</i>	Apostlebird			A		
	Corvidae	<i>Coloeus monedula</i>	Western jackdaw	128	13	A		
		<i>Corvus albicollis</i>	White-necked raven			A		
		<i>Corvus albus</i>	Pied crow			A/B		
		<i>Corvus capensis</i>	Black crow			A		Y
		<i>Corvus corax</i>	Common raven			A		Y
		<i>Corvus corone</i>	Carrion crow			A		
		<i>Corvus coronoides</i>	Australian raven			A		Y
		<i>Corvus frugilegus</i>	Rook			A		
		<i>Corvus splendens</i>	Indian house crow			A/B		
		<i>Cyanopica cyanus</i>	Azure-winged magpie			A		
		<i>Pica pica</i>	Common magpie			A		
		<i>Temnurus temnurus</i>	Ratchet-tailed treepie			A		
		<i>Urocissa erythroryncha</i>	Red-billed blue magpie			A		
	Cotingidae	<i>Rupicola peruvianus</i>	Andean cock-of-the-rock	65	1	A		
	Estrildidae	<i>Bathilda ruficauda</i>	Star finch	138	14	A/B		Y
		<i>Chloebia gouldiae</i>	Gouldian finch			A	Y	
		<i>Coccyzygia quartinia</i>	Yellow-bellied waxbill			A	–	
		<i>Erythrura trichroa</i>	Blue-faced parrotfinch			A/B	Y	
		<i>Estrilda astrild</i>	Common waxbill			A	Y	
		<i>Lonchura castaneothorax</i>	Chestnut-breasted mannikin			A/B	Y	
		<i>Neochmia phaeton</i>	Crimson finch			A	Y	
		<i>Neochmia temporalis</i>	Red-browed finch			A	Y	
		<i>Ortygospiza atricollis atricollis</i>	Black-faced quailfinch			A/B	Y	
		<i>Padda oryzivora</i>	Java sparrow			A	Y	
		<i>Poephila cincta</i>	Black-throated finch			A/B	Y	
		<i>Poephila personata</i>	Masked finch			A/B	Y	
		<i>Stagonopleura guttata</i>	Diamond firetail			A/B	Y	
		<i>Taeniopygia guttata</i>	Zebra finch			A/B	Y	
	Fringillidae	<i>Euphonia violacea</i>	Violaceous euphonia	229	1	A/B		
	Hirundinidae	<i>Hirundo neoxena</i>	Welcome swallow	86	1	A/B		
	Irenidae	<i>Irena puella</i>	Asian fairy-bluebird	2	1	A		

Table A1. Cont.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
	Leiothrichidae	<i>Garrulax bicolor</i>	Sumatran laughing thrush	143	3	A		
		<i>Leiothrix lutea</i>	Red-billed leiothrix			A		Y
		<i>Pterorhinus courtoisi</i>	Blue-crowned laughing thrush			A		
	Maluridae	<i>Malurus coronatus</i>	Purple-crowned fairywren	32	4	A		
		<i>Malurus cyaneus</i>	Superb fairywren			A/B		–
		<i>Malurus lamberti</i>	Variegated fairywren			A/B		Y
		<i>Malurus splendens</i>	Splendid fairywren			A/B		–
	Meliphagidae	<i>Acanthagenys rufogularis</i>	Spiny-cheeked honeyeater	189	15	A		
		<i>Anthochaera carunculata</i>	Red wattlebird			A		
		<i>Anthochaera chrysoptera</i>	Little wattlebird			A		
		<i>Anthochaera paradoxa</i>	Yellow wattlebird			A		–
		<i>Anthochaera phrygia</i>	Regent honeyeater			A		
		<i>Anthornis melanura</i>	New Zealand bellbird			A		
		<i>Entomyzon cyanotis</i>	Blue-faced honeyeater			A		
		<i>Lichenostomus melanops</i>	Yellow-tufted honeyeater			A		
		<i>Manorina melanocephala</i>	Noisy miner			A		
		<i>Manorina melanophrys</i>	Bell miner			A		
		<i>Meliphaga lewinii</i>	Lewin's honeyeater			A/B		Y
		<i>Philemon citreogularis</i>	Little friarbird			A		
		<i>Philemon corniculatus</i>	Noisy friarbird			A		
		<i>Phylidonyris novaehollandiae</i>	New Holland honeyeater			A/B		
		<i>Plectorhyncha lanceolata</i>	Striped honeyeater			A		–
	Menuridae	<i>Menura novaehollandiae</i>	Superb lyrebird	2	1	A/B		
	Momotidae	<i>Momotus coeruliceps</i>	Blue-crowned motmot	14	1	A		Y
	Monarchidae	<i>Grallina cyanoleuca</i>	Magpie-lark	100	1	A		
	Motacillidae	<i>Anthus novaeseelandiae</i>	Australasian pipit	69	1	A		Y
	Muscicapidae	<i>Copsychus malabaricus</i>	White-rumped shama	345	1	A		
	Nectariniidae	<i>Chalcomitra adelberti</i>	Buff-throated sunbird	143	4	A		
		<i>Cinnyris chalybeus</i>	Southern double-collared sunbird			A		–

Table A1. Cont.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
		<i>Cinnyris coccinigastrus</i>	Splendid sunbird			A		
		<i>Cinnyris jugularis</i>	Olive-backed sunbird			A/B		–
	Oreoicidae	<i>Oreoica gutturalis</i>	Crested bellbird	3	1	A		Y
	Oriolidae	<i>Oriolus auratus</i>	African golden oriole	38	5	A		Y
		<i>Oriolus chinensis</i>	Black-naped oriole			A		Y
		<i>Oriolus sagittatus</i>	Olive-backed oriole			A		Y
		<i>Sphecotheres vieilloti</i>	Australasian figbird			A		
		<i>Sphecotheres viridis</i>	Green figbird			A		
	Pachycephalidae	<i>Colluricincla harmonica</i>	Grey shrike-thrush	63	3	A		
		<i>Pachycephala pectoralis</i>	Australian golden whistler			A		
		<i>Pachycephala rufiventris</i>	Rufous whistler			A		
	Paradisaeidae	<i>Paradisaea minor</i>	Lesser bird-of-paradise	42	2	A/B		
		<i>Paradisaea apoda</i>	Greater bird-of-paradise			A		Y
	Passeridae	<i>Passer domesticus</i>	House sparrow	43	2	A		Y
		<i>Passer melanurus</i>	Cape sparrow			A		Y
	Petroicidae	<i>Eopsaltria australis</i>	Eastern yellow robin	49	1	A		
	Pittidae	<i>Pitta versicolor</i>	Noisy pitta	46		A		
	Ploceidae	<i>Euplectes franciscanus</i>	Northern red bishop	123	4	A		
		<i>Foudia madagascariensis</i>	Red fody			A/B		
		<i>Ploceus castaneiceps</i>	Taveta weaver			A		–
		<i>Ploceus cucullatus</i>	Village weaver			A/B		
	Pomatostomidae	<i>Pomatostomus superciliosus</i>	White-browed babbler	5	1	A/B		
	Prunellidae	<i>Prunella modularis</i>	Dunnock	12	1	A/B		–
	Psophophidae	<i>Psophodes occidentalis</i>	Chiming wedgebill	5	2	A		
		<i>Psophodes olivaceus</i>	Eastern whipbird			A/B		
	Ptilonorhynchidae	<i>Ailuroedus crassirostris</i>	Green catbird	27	3	A		
		<i>Ptilonorhynchus violaceus</i>	Satin bowerbird			A		
		<i>Sericulus chrysocephalus</i>	Regent bowerbird			A		
	Pycnonotidae	<i>Pycnonotus cafer</i>	Red-vented bulbul	151	1	A/B		
		<i>Pycnonotus jocosus</i>	Red-whiskered bulbul			A/B		
	Rhipiduridae	<i>Rhipidura albiscapa</i>	Grey fantail	54	2	A		
		<i>Rhipidura leucophrys</i>	Willy wagtail			A		
	Sturnidae	<i>Acridotheres fuscus</i>	Jungle myna	125	13	A		Y
		<i>Acridotheres tristis</i>	Indian myna			A		Y

Table A1. Cont.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
		<i>Aplonis metallica</i>	Metallic starling			A		
		<i>Cinnyricinclus leucogaster</i>	Violet-backed starling			A		Y
		<i>Gracula religiosa</i>	Common hill myna			A		
		<i>Lamprotornis bicolor</i>	African pied starling			A		
		<i>Lamprotornis iris</i>	Emerald starling			A		
		<i>Lamprotornis regius</i>	Golden-breasted starling			A		Y
		<i>Lamprotornis superbus</i>	Superb starling			A/B		
		<i>Leucopsar rothschildi</i>	Bali myna			A		Y
		<i>Mino dumontii</i>	Yellow-faced myna			A		Y
		<i>Onychognathus morio</i>	Red-winged starling			A		
		<i>Sturnus vulgaris</i>	Common starling			A		
	Thraupidae	<i>Paroaria coronata</i>	Red-crested cardinal	382	4	A		Y
		<i>Ramphocelus carbo</i>	Silver-beaked tanager			A		
		<i>Ramphocelus bresilius</i>	Brazilian tanager			A/B		–
		<i>Tachyphonus rufus</i>	White-lined tanager			A		
	Troglodytidae	<i>Troglodytes troglodytes</i>	Eurasian wren	86	1	B	Y	
	Turdidae	<i>Geokichla citrina</i>	Orange-headed thrush	175	3	A		Y
		<i>Turdus merula</i>	Eurasian blackbird			A		Y
		<i>Turdus philomelos</i>	Song thrush			A		
	Zosteropidae	<i>Zosterops lateralis</i>	Silvereye	143	1	A		
Pelecaniformes	Ardeidae	<i>Ardea alba</i>	Great egret	68	11	A		Y
		<i>Ardea cinerea</i>	Grey heron			A		Y
		<i>Ardea melanocephala</i>	Black-headed heron			A		Y
		<i>Ardea purpurea</i>	Purple heron			A/B		Y
		<i>Bubulcus ibis</i>	Cattle egret			A		Y
		<i>Egretta garzetta</i>	Little egret			A		Y
		<i>Egretta novaehollandiae</i>	White-faced heron			A		Y
		<i>Egretta picata</i>	Pied heron			A		Y
		<i>Egretta sacra</i>	Pacific reef heron			A		
		<i>Nycticorax caledonicus</i>	Nankeen night heron			A		
		<i>Nycticorax nycticorax</i>	Black-crowned night heron			A		
	Pelecanidae	<i>Pelecanus conspicillatus</i>	Australian pelican	8	5	A		Y
		<i>Pelecanus crispus</i>	Dalmatian pelican			A		Y
		<i>Pelecanus occidentalis</i>	Brown pelican			A		Y
		<i>Pelecanus onocrotalus</i>	Great white pelican			A		Y
		<i>Pelecanus thagus</i>	Peruvian pelican			A/B		Y

Table A1. Cont.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
	Scopidae	<i>Scopus umbretta</i>	Hamerkop	1	1	A		
	Threskiorthithidae	<i>Bostrychia hagedash</i>	Hadada ibis	36	11	A		
		<i>Eudocimus ruber</i>	Scarlet ibis			A		
		<i>Geronticus calvus</i>	Southern bald ibis			A/B		
		<i>Geronticus eremita</i>	Northern bald ibis			A		Y
		<i>Platalea ajaja</i>	Roseate spoonbill			A/B		Y
		<i>Platalea alba</i>	African spoonbill			A		Y
		<i>Platalea regia</i>	Royal spoonbill			A		Y
		<i>Plegadis falcinellus</i>	Glossy ibis			A		
		<i>Theristicus caudatus</i>	Buff-necked ibis			A		
		<i>Theristicus melanopis</i>	Black-faced ibis			A		
		<i>Threskiornis molucca</i>	Australian white ibis			A		Y
Phoenicopteriformes	Phoenicopteridae	<i>Phoenicopus chilensis</i>	Chilean flamingo	6	3	A		
		<i>Phoenicopus roseus</i>	Greater flamingo			A		
		<i>Phoenicopus ruber</i>	American flamingo			A		
Phaethontiformes	Phaethontidae	<i>Phaethon aethereus</i>	Query red-billed tropic bird	3	1	B		
Piciformes	Ramphastidae	<i>Ramphastos toco</i>	Toco toucan	36	7	A/B		
	Ramphastidae	<i>Ramphastos tucanus</i>	Red-billed toucan			A/B		
	Ramphastidae	<i>Aulacorhynchus haematopygus</i>	Crimson-rumped toucanet			B		
	Ramphastidae	<i>Aulacorhynchus caeruleogularis</i>	Blue-throated toucanet			B		
	Ramphastidae	<i>Pteroglossus castanotis</i>	Chestnut-eared aracari			B		
	Ramphastidae	<i>Pteroglossus frantzii</i>	Fiery-billed aracari			B/B		
	Ramphastidae	<i>Pteroglossus beauharnaisii</i>	Curl-crested aracari			B		
	Lybiidae	<i>Lybius dubius</i>	Bearded barbet	41	2	A/B		Y
		<i>Trachyphonus erythrocephalus</i>	Red-and-yellow barbet			A/Y		Y
	Picidae	<i>Dryocopus pileatus</i>	Pileated woodpecker	233	11	B	Y	
		<i>Dryocopus martius</i>	Black woodpecker			B	Y	
		<i>Geococcyx velox</i>	Lesser roadrunner			B		
		<i>Jinx torquilla</i>	Eurasian wryneck			B	Y	
		<i>Melanerpes formicivorus</i>	Acorn woodpecker			B	Y	
		<i>Mulleripicus fulvus</i>	Ash woodpecker			B	Y	
		<i>Piculus chrysocloros</i>	Golden-green woodpecker			B	Y	
		<i>Picus viridis</i>	Eurasian green woodpecker			A/B	Y	
		<i>Picumnus innominatus</i>	Speckled piculet			B	Y	

Table A1. Cont.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
Podargiformes	Podargidae	<i>Podargus strigoides</i>	Tawny frogmouth	16	1	A	Y	
Podicipediformes	Podicipedidae	<i>Tachybaptus novaehollandiae</i>	Australasian grebe	22	3	A		
		<i>Podiceps grisegena</i>	Red-necked grebe			B		
		<i>Podiceps nigricollis</i>	Eared grebe			B		
Procellariiformes	Diomedidae	<i>Diomedea exulans</i>	Wandering albatross	15	1	B		Y
Psittaciformes	Cacatuidae	<i>Cacatua galerita</i>	Sulphur-crested cockatoo	21	10	A	Y	
		<i>Cacatua sanguinea</i>	Little corella			A	Y	
		<i>Cacatua tenuirostris</i>	Long-billed corella			A	Y	
		<i>Callocephalon fimbriatum</i>	Gang-gang cockatoo			A	Y	
		<i>Calyptorhynchus banksii</i>	Red-tailed black cockatoo			A	Y	
		<i>Eolophus roseicapilla</i>	Galah			A	Y	
		<i>Lophochroa leadbeateri</i>	Major Mitchell's cockatoo			A	Y	
		<i>Nymphicus hollandicus</i>	Cockatiel			A	Y	
		<i>Zanda funerea</i>	Yellow-tailed black cockatoo			A	Y	
		<i>Zanda baudinii</i>	Baudin's black cockatoo			A	Y	
	Psittacidae	<i>Amazona aestiva</i>	Turquoise-fronted amazon	175	12	A	Y	
		<i>Ara ararauna</i>	Blue-and-gold macaw			A	Y	
		<i>Ara chloropterus</i>	Red-and-green macaw			A	Y	
		<i>Aratinga jandaya</i>	Jandaya parakeet			A	Y	
		<i>Aratinga nenday</i>	Nanday parakeet			A	Y	
		<i>Aratinga solstitialis</i>	Sun parakeet			A	Y	
		<i>Melopsittacus undulatus</i>	Budgerigar			A	Y	
		<i>Myiopsitta monachus</i>	Monk parakeet			A	Y	
		Genus <i>Amazona</i>	Amazon parrot			A/B	Y	
		<i>Psittacula krameri</i>	Rose-ringed parakeet			A	Y	
	Psittaculidae	<i>Psittacus erithacus</i>	African grey parrot			A	Y	
		<i>Pyrhura molinae</i>	Green-cheeked parakeet			A	Y	
		<i>Agapornis personatus</i>	Yellow-collared lovebird	190	36	A	Y	
		<i>Alisterus scapularis</i>	Australian king parrot			A	Y	
		<i>Aprosmictus erythropterus</i>	Red-winged parrot			A	Y	
		<i>Barnardius zonarius</i>	Australian ringneck			A	Y	
		<i>Coracopsis barklyi</i>	Seychelles black parrot			A	Y	
		<i>Cyclopsitta diophthalma</i>	Double-eyed fig parrot			A	Y	

Table A1. Cont.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
		<i>Genus Cyanoramphus</i>	Kakariki parrot			A	Y	
		<i>Eclectus roratus</i>	Eclectus parrot			A	Y	
		<i>Glossopsitta concinna</i>	Musk lorikeet			A	Y	
		<i>Lorius chlorocercus</i>	Yellow-bibbed lory			A	Y	
		<i>Lorius garrulus</i>	Chattering lory			A	Y	
		<i>Lorius lory</i>	Black-capped lory			A	Y	
		<i>Neophema chrysostoma</i>	Blue-winged parrot			A	Y	
		<i>Neophema pulchella</i>	Turquoise parrot			A	Y	
		<i>Neophema splendida</i>	Scarlet-chested parrot			A	Y	
		<i>Neopsephotus bourkii</i>	Bourke's parrot			A	Y	
		<i>Northiella narethae</i>	Naretha bluebonnet			A	Y	
		<i>Platycercus elegans</i>	Crimson rosella			A	Y	
		<i>Platycercus eximius</i>	Eastern rosella			A	Y	
		<i>Polytelis alexandrae</i>	Princess parrot			A	Y	
		<i>Psephotus haematonotus</i>	Red-rumped parrot			A	Y	
		<i>Trichoglossus chlorolepidotus</i>	Scaly-breasted lorikeet			A	Y	
		<i>Trichoglossus moluccanus</i>	Rainbow lorikeet			A	Y	
		<i>Platycercus adscitus</i>	Pale-headed rosella			A	Y	
		<i>Platycercus caledonicus</i>	Green rosella			A	Y	
		<i>Polytelis anthopeplus</i>	Regent parrot			A	Y	
		<i>Polytelis swainsonii</i>	Superb parrot			A	Y	
		<i>Pseudeos fuscata</i>	Dusky lory			A	Y	
		<i>Psittacula alexandri</i>	Red-breasted parakeet			A	Y	
		<i>Psittacula cyanocephala</i>	Plum-headed parakeet			A	Y	
		<i>Psittacula eupatria</i>	Alexandrine parakeet			A	Y	
		<i>Psittacula krameri</i>	Rose-ringed parakeet			A	Y	
		<i>Psittaculoides versicolor</i>	Varied lorikeet			A	Y	
		<i>Trichoglossus chlorolepidotus</i>	Scaly-breasted lorikeet			A	Y	
		<i>Trichoglossus moluccanus</i>	Rainbow lorikeet			A	Y	
		<i>Trichoglossus rubritorquis</i>	Red-collared lorikeet			A	Y	
	Strigopidae	<i>Nestor meridionalis</i>	Kākā	4	2	A	Y	
		<i>Nestor notabilis</i>	Kea			A	Y	
Pteroclitiformes	Pteroclitidae	<i>Pterocles orientalis</i>	Black-bellied sandgrouse	16	1	B	Y	
Rheiformes	Rheidae	<i>Rhea americana</i>	Greater rhea	2	2	A/B		

Table A1. Cont.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
Sphenisciformes	Spheniscidae	<i>Rhea pennata</i>	Darwin's rhea			A/B		
		<i>Spheniscus demersus</i>	African penguin	18	6	A		
		<i>Aptenodytes patagonicus</i>	King penguin			A		
		<i>Eudyptes chrysocome</i>	Southern rockhopper			A/B		
		<i>Eudyptes chrysolophus</i>	Macaroni penguin			A/B		
		<i>Eudyptula minor</i>	Little penguin			A		
		<i>Spheniscus humboldti</i>	Humboldt penguin			A		
Steatornithiformes	Steatornithidae	<i>Steatoris caripensis</i>	Oilbird			B		Y
Strigiformes	Strigidae	<i>Athene cunicularia</i>	Burrowing owl	228	24	A	Y	
		<i>Athene noctua</i>	Little owl			A	Y	
		<i>Bubo africanus</i>	Spotted eagle-owl			A	Y	
		<i>Bubo bengalensis</i>	Indian eagle-owl			A/B	Y	
		<i>Bubo bubo</i>	Eurasian eagle-owl			A	Y	
		<i>Bubo capensis</i>	Cape eagle-owl			A	Y	
		<i>Bubo lacteus</i>	Verreaux's eagle-owl			A	Y	
		<i>Bubo scandiacus</i>	Snowy owl			A	Y	
		<i>Bubo virginianus</i>	Great horned owl			A	Y	
		<i>Glaucidium perlatus</i>	Pearl-spotted owlet			A	Y	
		<i>Ketupa ketupu</i>	Buffy fish owl			A	Y	
		<i>Ninox boobook</i>	Australian boobook			A	Y	
		<i>Ninox connivens</i>	Barking owl			A	Y	
		<i>Ninox novaeseelandiae</i>	Morepork			A	Y	
		<i>Ninox rufa</i>	Rufous owl			A/B	Y	
		<i>Ninox strenua</i>	Powerful owl			A	Y	
		<i>Ptilopsis granti</i>	Southern white-faced owl			A	Y	
		<i>Strix aluco</i>	Tawny owl			A	Y	
		<i>Strix leptogrammica</i>	Brown wood owl			A	Y	
		<i>Strix nebulosa</i>	Great grey owl			A	Y	
		<i>Strix seloputo</i>	Spotted wood owl			A	Y	
		<i>Strix uralensis</i>	Ural owl			A	Y	
		<i>Strix woodfordii</i>	African wood owl			A/B	Y	
		<i>Surnia ulula</i>	Northern hawk owl			A	Y	
	Tytonidae	<i>Tyto alba</i>	Barn owl	18	5	A	Y	
		<i>Tyto longimembris</i>	Eastern grass owl			A	Y	
		<i>Tyto multipunctata</i>	Lesser sooty owl			A/B	Y	
		<i>Tyto novaehollandiae</i>	Masked owl			A	Y	
Struthioniformes	Struthionidae	<i>Struthio camelus</i>	Common ostrich	2	1	A		
Suliformes	Sulidae	<i>Morus capensis</i>	Cape gannet	10	1	A		

Table A1. Cont.

Order	Family	Species	Common Name	F	S	A/B	FUL	PUL
	Phalacrocoracidae	<i>Phalacrocorax capensis</i>	Cape cormorant	40	5	A		
		<i>Phalacrocorax neglectus</i>	Bank cormorant			A		
		<i>Phalacrocorax punctatus</i>	Spotted shag or pārekareka			A		
		<i>Phalacrocorax sulcirostris</i>	Little black cormorant			A		
		<i>Phalacrocorax varius</i>	Australian pied cormorant			A		
	Anhingidae	<i>Anhinga novaehollandiae</i>	Australian darter	4	1	A		
Tinamiformes	Tinamidae	<i>Eudromia elegans</i>	Elegant crested tinamou	46	1	A/B		Y
Trogoniformes	Trogonidae	<i>Trogon bairdii</i>	Baird's trogon	43	1	B		Y

Table A2. Types of blink in crocodilia, NMBI: nictitating membrane blink; GI R: globe retraction; LLBI: lower lid blink; Y: yes.

Order	Family	Species	Common Name	NMBI, GI R	NMBI	NMBI, LLBI, GI R	LLBI, GI R	NMBI, LLBI
Crocodylia								
	Alligatoridae							
		<i>Alligator mississippiensis</i>	American alligator		Y	Y	Y	
		<i>Caiman latirostris</i>	Broad-snouted caiman			Y		
		<i>Melanosuchus niger</i>	Black caiman			Y		
		<i>Paleosuchus palpebrosus</i>	Cuvier's dwarf caiman			Y		
		<i>Paleosuchus trigonatus</i>	Schneider's dwarf caiman	Y				
	Crocodylidae							
		<i>Crocodylus hombifer</i>	Cuban crocodile			Y		
		<i>Crocodylus johnstoni</i>	Freshwater crocodile	Y		Y	Y	
		<i>Crocodylus mindorensis</i>	Philippine crocodile	Y				
		<i>Crocodylus niloticus</i>	Nile crocodile			Y		
		<i>Crocodylus porosus</i>	Saltwater crocodile	Y	Y	Y		
		<i>Crocodylus siamensis</i>	Siamese crocodile			Y		
		<i>Mecistops cataphractus</i>	West African slender-snouted crocodile		Y	Y	Y	
		<i>Osteolaemus tetraspis</i>	West African dwarf crocodile				Y	
	Gavialidae							
		<i>Gavialis gangeticus</i>	Gharial		Y			Y
		<i>Tomistoma schlegelii</i>	Tomistoma			Y		

Table A3. Phylogeny of avian blink. Non-coding topology for Neoaves adapted from Braun and Kimball [25]. Clade I: core landbirds or Telluraves; Clade II: core waterbirds or Aequornithes; Clade III: Phaethontimorphae; Clade IV: Otidimorphae; Clade V: Strisores; Clade VI: Columbimorphes; Clade VII: Mirandornithes. ☒: Present.

Clade	Order	Most or All Families with Full Upper Lid Blinks	Some Families with Full Upper Lid Blinks	Families with Full Upper Lid Blinks	Some Families with Partial Upper Lid Blinks	Families with Partial Upper Lid Blinks
I	Passerines		<input checked="" type="checkbox"/>	Estrildidae, Troglodytidae		
I	Parrots	<input checked="" type="checkbox"/>				
I	Falcons					
I	Seriemas					
I	Rollers					
I	Woodpeckers	<input checked="" type="checkbox"/>				
I	Hornbills					
I	Trogons				<input checked="" type="checkbox"/>	
I	Cuckoo-roller					
I	Mousebirds				<input checked="" type="checkbox"/>	
I	Owls	<input checked="" type="checkbox"/>				
I	Hawks and eagles				<input checked="" type="checkbox"/>	
I	New World vultures				<input checked="" type="checkbox"/>	
II	Pelicans				<input checked="" type="checkbox"/>	
II	Cormorants					
II	Storks				<input checked="" type="checkbox"/>	
II	Penguins					
II	Tubenoses					
II	Loons					
III	Sunbittern					
III	Tropicbirds					
V	Hummingbirds	<input checked="" type="checkbox"/>				
V	Swifts	<input checked="" type="checkbox"/>				
V	Owlet-Nightjars	<input checked="" type="checkbox"/>				
V	Frogmouths	<input checked="" type="checkbox"/>				
V	Oilbird	<input checked="" type="checkbox"/>				
V	Potoos	<input checked="" type="checkbox"/>				
V	Nightjars	<input checked="" type="checkbox"/>				
	Shorebirds				<input checked="" type="checkbox"/>	Turnicidae
	Cranes and rails					
IV	Turacos				<input checked="" type="checkbox"/>	
IV	Bustards				<input checked="" type="checkbox"/>	
IV	Cuckoos					

Table A3. Cont.

Clade	Order	Most or All Families with Full Upper Lid Blinks	Some Families with Full Upper Lid Blinks	Families with Full Upper Lid Blinks	Some Families with Partial Upper Lid Blinks	Families with Partial Upper Lid Blinks
VI	Doves	☑				
VI	Mesites					
VI	Sandgrouse					
VII	Flamingos					
VII	Grebes					
	Landfowl		☑	Phasianidae		
	Waterfowl					
	Tinamous				☑	
	Emu and cassowaries					
	Kiwis					
	Rheas					
	Ostriches					
	Crocodylians (OUTGROUP)					

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