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'Body morphing' enables forest dwelling birds to master dense foliage with impunity: a novel avian flight performance*

'Body morphing' lässt Vögel dichtes Laubwerk meistern: ein neues Flugmanöver

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Abstract. Forest dwelling birds of a large number of taxa master the non-trivial task of navigating oftentimes dense foliage without colliding with the myriad of obstacles in their way. This hitherto unexplained feat of bird flight can be basically accounted for by two mechanistic hypotheses. The 'body morphing' hypothesis holds that the bird minimises the cross-section of its body when facing an obstacle or an opening too small to pass through with flapping wings. The 'planned trajectory' hypothesis suggests that the bird compromises the shortest distance to a goal by navigating the foliage with more detours than would be economically optimal in terms of distance flown. The posture minimising the cross-section of the body in flight is the passive phase of 'bounding flight' during which phases of wing flapping alternate with phases of sleeking the wings to the body. Observations of passerines negotiating the defined geometry of a net in a Philippine upland forest demonstrate that they can adjust the length of the passive phase such that 'body morphing' at the right time permits them to slip unharmed through commensurate openings and, by implication, also the foliage of their environment. The considerable individual variation of this performance is functionally discussed along the accumulating evidence of spider webs (*Nephila* sp., *Nephilengys* sp.) forming an as yet unappreciated source of mortality in the tropics.

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Keywords: Avian flight, flight maneuverability, forest-dwelling passerine, mortality, spider-web

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Introduction

Since long man has marvelled at the breath-taking performance of forest birds flying through dense foliage without colliding with the myriad of obstacles in their way. This feat has remained unexplained and has even gone unmentioned in treatises of bird flight (PENNYCUICK 1985, RAYNER 1985, WELTY & BAPTISTA 1988, MOORE & BIRKHEAD 1991). To account for the often twisted flight path of a bird passing through dense canopy two mechanistic hypotheses come to mind. First, the ‘planned trajectory’ hypothesis posits that before taking off the bird plans its trajectory upon detailed scrutiny of the obstacles and openings on its way subject to the sensory constraints in perceiving them; the bird then chooses a path that allows unimpeded flight. Obstacles only perceived at short distance, not at take-off, force the bird to circumnavigate them and resume the trajectory chosen before take-off, thus imposing costs of time and energy. Second, the ‘body-morphing’ hypothesis assumes that the bird approaches its goal more directly by adjusting its cross-section to the demands of obstacles such as twiglets, leaves, plant fibres and the like in its way, i. e. minimizing it when facing an opening too small while flapping wings to pass through. The best candidate for minimizing its cross-section is the sleeked-wings or passive phase of the ‘bounding flight’, one of two modes of intermittent flight in birds. During this ‘bounding flight’ the undulations come about by a phase of wing flapping propelling the bird through a ‘valley’ followed by a passive phase along a ‘mountain’ following a ballistic path (MOORE & BIRKHEAD 1991); in this passive phase the wings are closed (sleeked). Additionally, the ratio of active to still phases may depend on flight speed and increases with body size (TOBALSKE 2001), and in small forest-dwellers the active phase of wing-flapping may often prevail at the expense of the still phase, i.e. they scarcely flap-bound (E. C. pers. observation). (It should be noted that ‘body morphing’ as operationally and implicitly defined above differs from the more loose usage of the term in accounts of bird flight denoting any associated change of body shape as compared to aircraft [DIAL 2004].)

In a model based on energy savings through muscular work and on the aerodynamics of a flying projectile (airplane, bird) RAYNER (1985) could satisfactorily explain the wide occurrence of intermittent flight in birds. Moreover, the model can also account for the distribution across bird taxa of the two modes of intermittent flight, the second one being the 'undulating flight' in which a phase of wing flapping is followed by a phase of gliding with outstretched wings. Accordingly the vast majority of forest dwellers up to the approximate size of a Green Woodpecker is exercising 'bounding flight', dependent also on the wing area and the aspect ratio of the wing. (The terminology is somewhat unfortunate since the 'bounding flight' is even more undulating than the 'undulating flight'.) KIPP (1950) observed a correlation between living in dense environments and 'bounding flight' arguing that since steep ascents with continuous wing flapping and steep descents with sleeked wings are common in this habitat the bird maintains the habit of using the two phases when flying level along an unimpeded path. However, KIPP gave no reasons why the bird should behave this way. Furthermore, even during steep ascent complete wing sleeking does occur as evidenced by bird photography (MOORE & BIRKHEAD 1991).

For 'body morphing' to occur the bird when navigating a dense environment would have to change the duration and/ or the number of wing beats in the flapping phase, thus deviating from the species-specific ratio of the flapping phase to the still phase that is often 1:1 (MOORE & BIRKHEAD 1991) when moving along an unimpeded path. Aside from this need for timing another need arises from precisely aligning the body axis to the constraining opening by the last wing beat(s) before closing the wings, largely by changing yaw and pitch. This latter correction may slightly compromise the maximal economy of a path.

We will argue here for the 'body-morphing' hypothesis. It predicts that the bird when facing relatively small openings in its flight path can time its passive phase of the (bounding) flight accordingly and keep clear from their boundaries. The responses of birds to perlon mist nets in a Philippine upland forest permitted us to examine this hypothesis, with the Philippine bulbul (*Hypsipetes philippinus*), a thrush-sized passerine and agile flier, being at centre stage.

Method

The study area is a mosaic of primary and second growth forest in the upland (450m asl.) of the NW Panay Peninsula near Research Station Sibaliw of the PESCP. In this area, the Philippine Bulbul is the most common bird featuring 50% of all mist net captures. For observing how Bulbuls fare with mesh sizes too large to catch them, but small enough to look at their presumed capability of mastering small openings in the canopy mist nets of the largest size available were put up in forest clearings with Bulbul 'traffic' in the canopy. Nets of mesh size 62x62mm, with the squares 'standing' on a corner,

were erected covering an area from 2 to 10m above ground in two clearings; alignment of the nets divided the clearings midway, 2-3m and 4-6m distant, respectively, from either border of the understory canopy that exceeded the upper edge of either net by 2 and 3m, respectively. Observations covered both the dry and the rainy seasons throughout daytime from 2004 through 2007. Records pertain to birds that when coping with the net were not captured, with 32 of 34 all records being kept by one observer (E. C.). The latter was looking at the net from the ground 2m away from one end and slightly displaced away from the net's plane. Estimation of distances $\leq 0.8\text{m}$ were based on body length of the bird at stake (223mm), longer distances on the dimensions of the net. As expected no Bulbul was ever captured by the over-large meshes of the net.

Results

Net Observations

Failure of capture resulted from four basic behaviour styles, largely of Philippine Bulbul. A mere seven (23.3%) from among 30 Bubluls traversed the net smoothly, with no trace of an impact (Table 1, I.a). One of them could be clearly seen, against the sky, to sleek its wings to the body. Two more individuals passed similarly upon briefly perching in a mesh (II.b).

The majority of 27 more birds including four individuals of three more species did not pass the net, they were rather bumping into and then keeping clear of it, either passing around it or backing off, or by doing both in a row (II). When having detoured the net the birds settled down in the canopy after flying a mere 2-4m in the general direction of the previous flight path but with a translatory shift away from the previous path. They did *not* correct for this shift by returning back to their original path as postulated by the 'planned trajectory' hypothesis. A third alternative was avoiding any impact from a distance (III), though sometimes quite narrowly (III.a), then flying in various ways around the net, again with no translatory resumption of the previous flight path. In some instances birds backed off entirely (III.e). The detection distance implied in net avoidance could be discerned only during episodes involving stalling in mid-air (III), not when birds began climbing in the canopy away from the net to fly over it while crossing the forest gap (IV).

Tab. 1. Responses of Philippine Bulbul (*Hypsipetes philippinus*) and few other passerines to mist net (10m x 19m, 2m above ground) of mesh size 62x62mm in Philippine upland forest, 450m a.s.l.

Res- ponse class	Response of bird flying ± perpendicularly toward net	n observations (%)
I.a	Traverse, with 4 birds stalling at distances of 0.4, 0.6, 0.6 and ?m	7 (23.3)
I.b	Traverse upon perching in net	2 (6.7)
II.a	Bump into & perch in net, traverse	1 (3.3)
II.b	Bump into net, flung back by 0.2m while maintaining perpendicular alignment, traverse	1 (3.3)
II.c	Bump into net, back off, perch nearby, detour net horizontally	1 (3.3)
II.d	Bump into net, flung back by 0.8m, detour it vertically	1 (3.3)
II.e	Bump into & fly along net, bump into net where caught	1 ^a (3.3)
III.a	Stall clear of net by 5cm ^b , fly along, try traverse net again, detour it horizontally	1 (3.3)
III.b	Stall clear of net by from 0.1 to 4m ^b , detour net horizontally	5 ^c (13.3)
III.c	Dto., detour net vertically	1 (3.3)
III.d	Dto., reverse	3 (10.0)
III.e	Dto., fly along net & back off	3 ^d (6.7)
IV.	Ascend from >>4m & fly over net	7 ^e (13.3)
Total: Philippine Bulbul		30 (100.0)

^a Mesh size 36x36mm, net width only 5m.
^b Median 1.2m (n = 11 Bulbuls).
^c Including thrush-sized unidentified bird.
^d Including a flowerpecker (*Dicaeum* sp.).
^e Including 2 *Coracina striata* flying side by side.

Incidental Observations on net-free Conditions

In a bird's flight path oblong slits are much less taxing than openings resembling the net's meshes. Accordingly, and compatible with the 'body-morphing' hypothesis, is the agility of Tropicbird Hornbills (*Penelopides panini panini*) mastering a narrow vertical slit as in a building's door and a window of the width of their body with sleeked wings (ca 12cm). A female passed the slit full speed and a male with one wing stroke after taking off from a perch 0.6m away. The traversal must have occurred during the down-stroke of the wings since any phase of the up-stroke would have prohibited smooth

traversal. Moreover, since hornbills exercise undulating flight with gliding replacing the still phase of the bounding flight sleeking of the wings was no option (see also RAYNER 1985). It is noteworthy that the male's manoeuvre again bears out the fact that body-morphing can be achieved in only one wing beat, i.e. by reducing the *number* of beats of a flapping cycle to the irreducible minimum.

The 'body-morphing hypothesis' also predicts that with many obstacles impinging on the flying bird in quick succession the continuous forward progression should become staggered. This is in fact the case with a bird, e. g. a magpie (*Pica pica*), flying straight through a tree with many twigs occluding its path; the need to replace flapping with closing the wings many times imposes irregularities of progression otherwise not seen (E. C., pers. observation). This falsifies the 'planned-trajectory' hypothesis predicting a continuous progression at constant speed, and by implication supports 'body-morphing' to be the trick by which birds master flying straight through foliage of a forest.

Discussion

The mechanics of mastering small openings

The most striking feat of the bulbuls' coping with the net was traversing it with impunity. By what manoeuvre do they achieve this? The mesh measures maximally 88mm both horizontally and vertically, the Bulbul's wingspan ca 350mm. The width of the down stroke with fully unfolded wings during flapping flight ranges from appr. this latter value down to half of it and, thus, precludes this phase of the flapping cycle to allow traversal of the net. The smallest cross-section of the cycle would be the lifting of the nearly folded wings close to the body during the upstroke; specifically when the carpal joints are just reaching above the level of the crown. Seen from behind, this cross-section may be approximated by an upright rectangle (HERZOG 1968, RÜPPELL 1977). Based on the circumference of the body with sleeked wings, as measured in a live Bulbul, of 140mm, the spindle-like body's diameter is 44.6mm. Allowing conservatively for an additional 3cm due to the wings protruding from the body's contour during the upstroke (HERZOG 1968, RÜPPELL 1977) the rectangular cross-section would minimally attain 75mm in width, and accordingly the rectangle a height of ca 85mm. Accordingly the body would not pass through a mesh's square opening with vertical diagonal of 88mm. Hence, in no phase of the flapping cycle would the Bulbul achieve collision-free traversal of the net. This leaves only the smallest cross-section, i.e. of the sleeked-wings during the passive phase of bounding flight, to accomplish the trick: with a roughly circular cross-section of 1561sqmm (diameter 45mm, see above) the Bulbul can pass comfortably a square mesh of 3844sqmm. From this it follows that the time pattern of the wing beats during the active phase of the bounding flight is to be modified such that the bird is allowed to time its wing closing at the right moment, i. e. perform 'body

morphing'. By implication, this trick would permit a bird to negotiate comparable openings in dense foliage of the canopy.

One chance observation (Table 1, II.b) reveals the postulated change of pattern being accomplished by altering the number of wing beats: the distance from a 'take off' in mid air to the net afforded the time for only 1-2 wing beats. (The domestic pigeon can vary its wing beat frequency from 9.4/s at take off to 5.4/s at cruising speed, e. g. 12m/s [AULIE 1983].) There is no noticeable descent or ascent upon passing the net. This can only mean that any shortening or extending the flapping cycle dependent on the distance from the opening to be mastered must be compensated for upon traversal by a corresponding shortening or lengthening of the passive sleeked-wings phase. This conclusion is corroborated by net-free observations on magpies navigating a tangled environment where forward progression becomes staggered due to many obstacles in the path forcing the bird to interrupt the flapping phase of intermittent flight more often. The conclusion is further paralleled by hornbills mastering vertical slits in their environment by accurately timing the end of the down stroke of the wing in mid flight, the only flight phase in which the body fits through an opening of body width at rest; this again clearly excludes a planned trajectory that would allow the bird to pass openings of this kind only by chance.

The manoeuvres documented in Table 1 give some clue as to the reaction times of birds when confronting the net. One Bulbul when flung back by the net by 0.2m achieved a smooth traversal immediately thereafter (II.b). In cruising flight the similar-sized European Blackbird (*Turdus merula*) flies at speed of 13.3m/s which speed was probably undercut by the Bulbul whose new forward thrust from speed 0m/s was comparable to the lower speed of a bird at take off (HERZOG 1968). Assuming this latter speed to be 10m/s this individual accomplished perceiving the geometry of the net when starting a new approach and close its wings after 'take off' in mid-air, all in 20ms. This reaction time undercuts dramatically the looming response of the pigeon; time-to-collision with a looming object as measured by firing of looming-sensitive neurons to the peak of muscle activity is 80-100ms (WANG and FROST 1992) to which time period that from activating the retina to firing of those neurons would have to be added; the whole response time would appear to be $\gg 100$ ms. Measurements of time-to-collision due to self-motion of the bird in a static environment, the net-encounter problem of this note and the converse of looming, seem to be lacking.

The great majority of the birds stalled in front of the net or bumped in it, then kept clear of it in various ways (Table 1). Final avoidance was governed by physically keeping clear of the net rather than by fearful avoidance of some deadly risk; some avoided collision only narrowly (III.a, b). Even after impact, two from among 34 individuals traversed the net (II.a, b) while many others only narrowly avoided contact (II, III, IV). Hence, avoidance was governed by physical keeping clear of the net rather than by a fearful reversal of approach from some deadly risk, e. g. predation, though collision was certainly potentially harmful. The small proportion of birds traversing the net smoothly (I) indicates that this feat is rather taxing, but an alternative explanation is possible (see below).

Avoiding the net from a distance (Table 1, III.a – e) affords the unique opportunity to infer data on the visual acuity (minimum visible) without conditioning though illumination and a variable background must have increased response variation. The black perlon threads measure 0.5mm in diameter, the knots 1mm, with the threads thus undercutting most of the smallest obstacles in nature (twiglets, tendrils, peduncles). Since these never elicit any avoidance or stalling it must be the structure of the net as a whole that is repulsive. Should the knots be perceived as a coherent object pattern rather than as spatially isolated dots they might repulse birds before the threads would generate coherence. As the bird approaches the net the knots move simultaneously in roughly the same direction across each half of the visual field of the retinae. This movement may synchronize separate tectal groups of neurons and thus give rise to commonalities of neural excitation as when neighbouring receptive fields of the retina are stimulated simultaneously (NEUENSCHWANDER & VARELA 1993). These commonalities might translate into perceiving the knots as one obstacle rather than many separate objects. Assuming thus that it is the knots that make the birds stall the maximum stalling distance of 4m translates into a maximum detection distance of >4m. From this it follows the angle of resolution to be <34'' rather than <17'' if the knots rather than the threads would be the perceived obstacle pattern. Either value would be close to the lower bound (20'') measured for passerines so far (WELTY & BAPTISTA 1988). The still longer avoidance distances of some birds (IV) could be the result of birds previously learning to orient spatially toward the net as part of their home ranges (see BALDA & WILTSCHKO 1991) that in the Bulbul comprise many hectares (E. C., pers. observation). Great Tits (*Parus major*) on familiar ground as compared to novices on unfamiliar ground apparently learn the potential hiding places and escape routes to cope with an attacking hawk (P. J. Drent pers. communication). A similar fearful behaviour is shown by migrant birds when foraging in an unfamiliar stopover point (HAMPE & BAIRLEIN 2000). The many shorter stalling distances <4m (Table 1, III) are open to a number of interpretations, yet foremost the repelling effect of the threads per se.

Functional aspects of net avoidance

Neophobia (fear of novelty) may be one explanation of net avoidance, yet mistaking the net for a spider-web is another functional interpretation. Spider-webs have proven fatal on many occasions. Five birds on Panay Island including the Bulbul were caught in a spider's (*Nephila* sp., *Nephilengys* sp.) web. Further bird deaths in *Nephila* webs have been reported by GRAHAM (1997), RATHORE (2007), and SAKAI (2007). These webs lack ornaments that in other orb web spiders render a web conspicuous to forestall its damage (refs. in ALCOCK 2005). The inconspicuousness of the unadorned webs makes them dangerous. The idea of a mistaken identity of the net is underscored by the reasonable assumption of the pattern of threads being the effective repellent rather than the knots per se (see above) that, furthermore, do not generally typify a spider's

web. In addition, a flowerpecker backed away from the net irrevocably (III.e) though by virtue of its very small size it could have comfortably passed through, even during wing flapping. In consonance with this, a flowerpecker (*Dicaeum trigonostigma*) got fatally ensnared in the relatively weak web of *Nephilengys* sp. that, on another occasion,

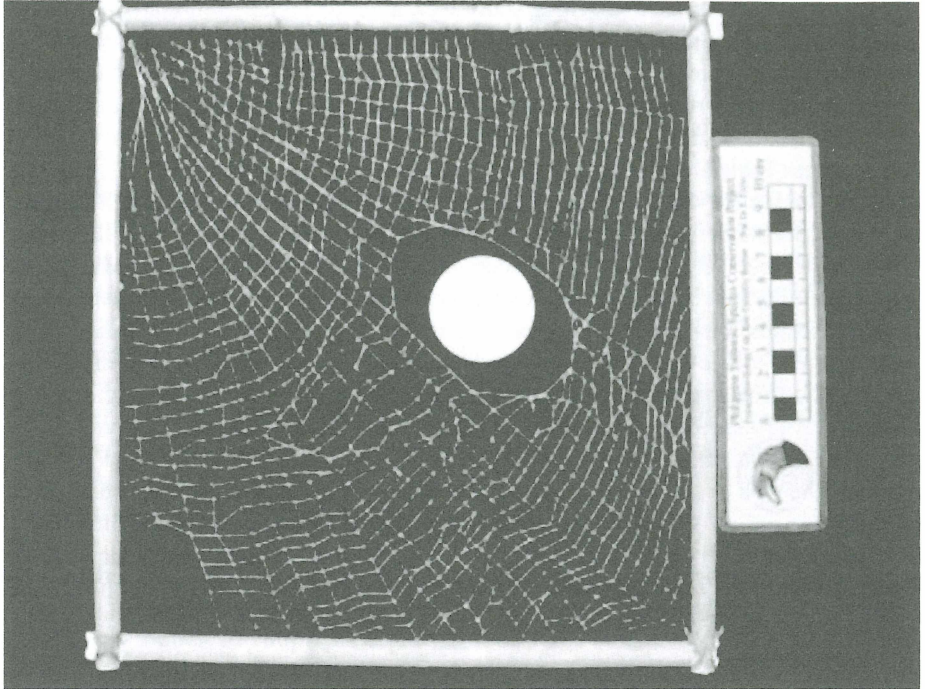


Fig. 1. Hole torn by a Philippine Bulbul passing a *Nephilengys* spider's web artificially attached to a wooden frame. Before its voluntary take off the bird was afforded the opportunity of screening the frame opening at leisure in a cage from a distance of 80cm. The white circle visualizes the sleeked-wings, proportional size cross-section of the bird in the still phase of bounding flight; any other flight phase would have made a bigger hole. Photo courtesy M. Gronwald, art work and contrast enhancement by Helga Schulze.

a Bulbul with 10 times the body mass penetrated with impunity though this bird was driven by the need to escape from artificial confinement (Fig. 1). Yet also four free ranging White-eared Brown-doves (*Phapitreron leucotis*) and a male Tarictic Hornbill with their still larger body masses were seen to plunge into the net without the slightest hesitation. These strong fliers would even pass with impunity the much stronger net of *Nephila* spiders. This correlation between body mass and net avoidance supports the mistaken identity idea of net avoidance by the smaller birds.

Given this risk, why then do Bulbuls repeat their attempts at traversal upon screening the net at close quarters or even after bumping into it? The expanse of any spider's web is minuscule as compared to the net, and a pre-programmed avoidance response should fail with a 'giant web' nowhere extant in nature. The avoidance appears to be tuned adaptively to orb-webs of typically limited spatial dimensions.

The mistaken identity idea provides, moreover, a better explanation than the novelty avoidance hypothesis for two seemingly disparate phenomena. First, by virtue of its very large surface area, colour (black vs. colourless) and its dimensions of elements (≥ 0.5 mm) the net's resemblance to a spider's web may be so imperfect that a marked proportion of birds 'falls prey' to the net by plunging into it. Second, the large variation of responses (Table 1, I through IV), most evident among the net avoiders (III), suggests natural selection for web avoidance to be weak for a strong and relatively large flier like the Bulbul for whom most webs would pose no real threat. The inverse correlation, as indicated above, between net avoidance and body mass mentioned would appear consonant with this reasoning. For a given species, novelty should be repulsive always or never. In birds, the overwhelming variance in fear of novel objects is due to taxonomic position, next to life-style and food specialization, all in all much less to individual variation (GREENBERG 1983, METTKE-HOFFMANN et al. 2002, METTKE-HOFFMANN et al. 2005). That there is strong selection for web avoidance for animals that are genuinely vulnerable such as small butterflies is born out by experiments with a small *Eurema* sp. (Pieridae). It avoids the web of *Nephilengys* sp. mentioned above from a distance with almost no individual variation (M. GRONWALD pers. communication), and larger butterflies of half a dozen species never traverse the large-meshed net used in this study; when incidentally flying toward it they change course just before touching it, usually flying on a detour around it (E. C. pers. observation).

Conclusion

The observations suggest the body-morphing hypothesis to be able to explain how fast flying birds master the tangled forest environment and thus to be superior to the planned trajectory hypothesis. Furthermore, the latter seems scarcely robust: a gust of wind would compromise any planned flight trajectory which is not what can be observed in nature. The considerable variation of coping-styles vis-à-vis a customized perlon net in the Philippine Bulbul is thought to arise from moderate selection against being trapped in potentially deadly spider-webs.

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Zusammenfassung

'Body morphing' lässt Vögel dichtes Laubwerk meistern: ein neues Flugmanöver. Waldbewohnende Vögel vieler Gruppen vollführen einen Bogenflug, der sie fallweise über lange Strecken geradeaus führt, ohne dass sie mit einem der zahllosen Hindernisse zusammenstoßen. Aktive Flugphasen mit Flügelschlag wechseln mit ungefähr ebenso langen passiven Phasen mit angelegten Flügeln ab. Beobachtungen an einem Sperlingsvogel, dem Philippinenbülbul (*Hypsipetes philippinus*), beim Passieren eines Japannetzes mit festliegender Maschengröße beweisen, dass er die Dauer der passiven Flugphase zeitlich so abstimmt, dass er infolge von 'body morphing', d. h., dem Minimieren des Körperquerschnitts zur rechten Zeit, ohne anzustoßen durch die Maschen fliegen kann. Auf die Natur übertragen heißt dies, dass der Vogel so auch durch dichtes Laubwerk manövrieren kann. Die individuell große Streuung des Einsatzes dieser Flugleistung am Netz wird im Rahmen der Meidung gefährlicher Spinnennetze und deren Verwechslung mit dem Japannetz erörtert. Stärkere Spinnennetze wie die von *Nephila spec.* und *Nephilengys spec.* erwiesen sich oft als tödlich für tropische Kleinvögel einschließlich des Philippinenbülbuls, dessen beträchtliche Körpergröße ihn aber gerade noch als gefährdet erscheinen lässt.

Tab. 1: Antworten des Philippinischen Bülbuls (*Hypsipetes philippinus*) und wenigen anderen Sperlingsvögeln auf Fangnetze (10 m x 19 m, 2 m über Grund) mit einer Maschenweite von 62 x 62 mm im philippinischen Hochland, 450 m ü.d.M.

Abb. 1.: Ein Loch, das von einem philippinischen Bülbül (*Hypsipetes philippinus*) gerissen wurde und an einem Spinnennetz von *Nephilengys* vorbeiführt, das künstlich an einem Holzrahmen befestigt ist. Vor dem freiwilligen Start hatte der Vogel die Möglichkeit, die Rahmenöffnung in einem Käfig aus einer Entfernung von 80 cm nach Belieben einzuschätzen. Der weiße Kreis visualisiert, den proportionalen Größenquerschnitt des Vogels in der schlagfreien Phase des Gleitfluges mit angelegten Flügeln; jede andere Flugphase hätte ein größeres Loch gemacht. Fotovorlage mit freundlicher Genehmigung von M. Gronwald. Grafikumsetzung Helga Schulze.

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