ORIGINAL ARTICLE

The Hindlimb Myology of *Tyto alba* (Tytonidae, Strigiformes, Aves)

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With 6 figures and 1 tables

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Summary

This work is the first myological dissection performed in detail on the hindlimb of *Tyto alba*. Six specimens were dissected and their muscle masses were obtained. *T. alba* has the classical myological pattern present in other species of Strigiformes, such as a well-developed *m. flexor digitorum longus* and the absence of the *m. plantaris, flexor cruris lateralis* and *ambiens*. Also, *T. alba* lacks the *m. extensor propius digiti III, m. extensor propius digiti IV* and *m. lumbricalis*, present in the Strigidae. Hindlimb muscle mass accounts for 14.13% of total body mass, which is within the range of values of both nocturnal (Strigiformes) and diurnal (Falconidae and Accipitridae) raptors. This study provides important information for future studies related to functional morphology and ecomorphology.

Introduction

The order Strigiformes is composed of nocturnal birds of prey, commonly known as owls. Two families are recognized, Tytonidae and Strigidae; the former comprises 27 species whereas the later comprises 223 species (König and Weick, 2008). Particularly, the Barn owl, *Tyto alba*, has a worldwide distribution, being one of the most widely distributed species of owls in the world (McCafferty and Lurcock, 2002). Barn owls feed on mammals, mainly rodents, and to a lesser extent on birds, insects, reptiles and amphibians (Bó et al., 2007).

Like all raptors, the barn owl uses its feet to catch, hold and carry other animals (Einoder and Richardson, 2006). Its claws are curved and the zygodactyl disposition of the toes maximizes the area of the foot, reducing the chance of prey escape (Payne, 1962). Also, the barn owl has well-developed digit flexor muscles (e.g. *m. flexor dig-itorum longus*, Goslow, 1972) and a distinctive tendon locking mechanism (Einoder and Richardson, 2006) in its toes.

Detailed internal anatomical information on owls is scarce, for instance, the hindlimb myology of Tytonidae has been less studied than that of the Strigidae. There are several studies considering the muscles and bones under a biomechanical perspective (*i.e.* Goslow, 1967;

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Ward et al., 2002; Einoder and Richardson, 2006; Backus et al., 2015). There are studies where the focus is a descriptive myology of the Owls, but they are not as many and, in those cases, the family considered is Strigidae and not Tytonidae (Garrod, 1873; Garrod, 1874; Hudson, 1937; Volkov, 2004). One of the first studies was the work of Garrod (1873) where mainly the presence and absence of muscles were described for 20 species of Strigidae. The works of Hudson (1937) or Volkov (2004) are complete descriptions of each muscle of the hindlimb, but in both cases only species from the family Strigidae were considered and no quantitative assessment was performed. In the former, Otus asio and Bubo virginianus were considered, whereas in the later seven species are described: Aegolius funereus, Asio flammeus, A. otus, Athene noctua, Glaucidium cuculoides, G. passerinum, Strix uralensis. Regarding the quantitative aspect, only Hartman (1961) studied the percentage of hindlimb muscle mass in the Tytonidae T. alba, among other Strigiformes.

The objective of this work was to perform a detailed description and a quantitative analysis of the hindlimb myology of *T. alba* and to compare it with the available information for other Strigiformes. These data will be useful both for comparative myological studies and for morpho-functional analyses.

Materials and Methods

A total of six specimens of *T. alba* were dissected. The materials came from Bariloche, Río Negro Province, Argentina. They were collected from Fundación Felix de Azara (Buenos Aires, Argentina) and Parque Nacional Nahuel Huapi (Rio Negro, Argentina permit number 1380). Materials were collected when they were found dead and in good condition of their musculature.

Materials were frozen and kept in freezer until their dissection. A classical description of the musculature of the hindlimb was performed by identifying each muscle, its origin and insertion site. The descriptions follow the order of appearance from superficial to deep muscles. The mass of each muscle (one limb considered) was measured to the nearest 0.01 g with a digital scale. The percentage of individual muscle masses with respect to the total hindlimb mass and the body mass were calculated. Also, the total mass of main flexors and extensors on each articulation was calculated and compared within the different joints (pelvic, knee, ankle and digits). The anatomical nomenclature follows Baumel et al. (1993). The long bones are abbreviated as TBT (tibiotarsus) and TMT (tarsometatarsus). The main actions of the muscles were taken from Goslow (1967) and George and Berger (1966).

Results

Description of the muscles

The *m. iliotibialis cranialis* (IC, Figs 1a,e and 2a,b) is the most superficial and anterior muscle of the cranial aspect of the pelvis. It has a fleshy origin on the ventral edge of the *ala preacetabularis illi*, a strap-like belly that goes to the medial aspect and a fleshy insertion on the *ligamentum patellae* and *crista cnemialis cranilis* of the tibiotarsus.

The *m. iliotibialis lateralis* (IL, Figs 1a and 2a) is posterior to the IC; it has an aponeurotic origin on the *crista iliaca dorsalis*, reaching the *acetabulum*; it also has a flat tendon that attaches the most anterior portion of the *crista dorsolateralis ilii* on the *vertex ilii* and on the most ventral and anterior portion of the *ala preacetabularis ilii*. The insertion is by a distal aponeurotic portion, closely related to the *M. femorotibialis lateralis et intermedius*, on the ligamentum patellae.

The *m. iliofibularis* (IF, Figs 1a,f and 2a) originates on the *crista dorsolateralis ilii* by a long fleshy origin with an aponeurotic portion on the medial aspect of the posterior half of the muscle. The IF tapers, showing its typical triangular shape and inserting on the *tuberculum m. iliofibularis* of the lateral surface of the fibula, after passing through the *ansa m. iliofibularis*. It passes between the



Fig. 1. *Tyto alba*, sketches of the pelvis in lateral view (a), right femur in anterior (b), lateral (c) and posterior (d) view and right tibiotarsus in anterior (d) and posterior (e) view. Origins are indicated with red and insertions with blue. Abbreviations of the muscles are in Table 1, scale bar: 1 cm.

pars lateralis and intermedia of the *m. gastrocnemius* with a robust tendon.

The *m. iliofemoralis externus* (IFE, Figs 1a,c and 3a) has a fleshy origin on the caudal end of the *crista dorso-lateralis ilii* and a tendinous insertion on the trochanter femoris.

The *m. iliofemoralis internus* (IFI, Fig. 1a,d) is one of the smallest muscles of the pelvis–femur joint, with a fleshy origin just anterior to the *foramen acetabuli*, near the ventral end of the *ilium* and a fleshy insertion on the proximal fourth of the medial aspect of the femur.



Fig. 2. Superficial muscles of the right hindlimb of *Tyto alba* in lateral (a) and medial (b) view. Abbreviations: (I), (m) and (i) represent the *pars* of the *m. gastrocnemius, lateralis, medialis* and *intermedius,* respectively, and the rest of the abbreviations of the muscles are in Table 1, scale bar: 1 cm.



Fig. 3. Deep muscles of the right hindlimb that originate on the pelvis in lateral view (a,b). Abbreviations of the muscles are in Table 1, scale bar: 1 cm.

The *m. flexor cruris medialis* (FCM, Figs 1a,f, 2a,b and 3b) is a strap-like muscle with a fleshy origin on the caudal portion of the ventral edge of the *ala ischii*. It inserts by a tendon on the medial aspect of the TBT after going through the *pars medialis* and *intermedia* of the *m. gastrocnemius*.

The *m. ilitrochantericus caudalis* (ITC, Figs 1a,c, 2a and 3a) has a fleshy pre-acetabular origin on the *fossa iliaca dorsalis* of the *ilium*. The insertion is by a thick, flat tendon on the *impressiones iliotrochantericae* in the lateral proximal facet of the femur. It covers the origin of the IL with its belly.

The *m. ilitrochantericus cranialis* and *m. ilitrochantericus medius* (ITCr + M, Figs 1a,c and 3a) are fused and their individual bellies cannot be identified. They arise by fleshy fibres on the ventral edge of the *fossa iliaca dorsalis* and a tendinous insertion on the lateral surface of the femoral trochanter, below the ITC.

The *m. ischiofemoralis* (ISF, Figs 1a,c and 3a) arises by fleshy fibres in the *ala ischii* and *lamina infracristalis ilii*, below the *crista dorsolateralis illi*. The insertion is with a tendon on the *trochanter femoris*.

The *m. puboischiofemoralis* (PIF, Figs 1a,d, 2b and 3a, b) arises by fleshy fibres along the ventral edge of the *ala ischii*. It has two bellies that insert by fleshy fibres on the caudal two-thirds of the femur; the medial portion also inserts on the *m. gastrocnemius pars intermedia*.

The *m. obturatorius lateralis* (OL, Figs 1a,c and 3b) arises by fleshy fibres beneath the *foramen obturatorium* and inserts by fleshy fibres on the lateral aspect of the proximal region of the femur, on the *impressiones obturatoriae*. It had both bellies that are separated with the tendon of the OM between them.

The *m. obturatorius medialis* (OM, Figs 1c and 3b) is an oval-shaped muscle located in the medial side of the pelvis, along the medial side of the *ala ischii* and the anterior half of the pubis. It arises by fleshy fibres and inserts by a stout tendon on the *trochanter femoris* after passing outward through the foramen obturatorum, inserting next to the OL.

The *m. caudofemoralis* (CF, Figs 1d and 3a) is represented only by the *pars caudalis and* is long and thin with a tendinous origin in the *aponeurosis cruciata* of the *m. depressor caudalis* at the base of the pygostylus. The insertion is tendinous on the proximal third on the posterior aspect of the femur; both tendons are small and slender.

The *m. femorotibialis lateralis* and *m. femorotibialis intermedius* (FTL + I, Figs 1b, 2b and 3a,b) cannot be individually identified although once removed from the femur the limit is defined on the medial aspect and also, on the femur expressed by the *linea intermuscularis cranialis*. They arise on the lateral and anterior aspect of the femoral shaft by a tendon and by fleshy fibres from the femur and insert on the *ligamentum patellae* by a wide aponeurosis.

The *m. femorotibialis medialis* (FTM, Figs 1d and 2a) originates by fleshy fibres by fleshy fibres in the medial part of the distal two-thirds of the shaft of the femur. It inserts by a tendon on the proximal epiphysis of the TBT, in the *crista cnemialis cranialis*.

The *m. fibularis brevis* (FB, Figs 1e, 2a, 4b and 5b) has one head of origin that arises by fleshy fibres on the fibula and on the TBT. The insertion of this muscle is by a robust tendon on the caudolateral side of the TMT, the *tuberculum m. fibularis brevis*.





Fig. 5. Deep muscles of the right hindlimb that originate on the distal epiphysis of the femur and tibiotarsus in anterior (a,b) and posterior (c,d) view. Abbreviations of the muscles are in Table 1, scale bar: 1 cm.

The *m. tibialis cranialis* (TC, Figs 1b, 2a,b and 4a) is the most superficial muscle of the anterior aspect of the TBT and is well developed in this species. It has two bellies, the *caput tibiale* that has a fleshy origin between the *cristae cnemialis cranialis* and *lateralis*, whereas the *caput femorale* originates by tendon in the *condylus*

Fig. 4. *Tyto alba*, sketches of the right tarsometatarsus and digits in anterior (a) and posterior (b) view. Origins are indicated with red and insertions with blue. Abbreviations of the muscles are in Table 1, scale bar: 1 cm.



Fig. 6. Sum of the muscles based on the average mass of each muscle across all specimens (in g) of the hindlimb grouped by articulation and main action (flexion or extension).

lateralis of the femur, in the *fovea tendineus m. tibialis cranialis*. Both bellies fuse together and the insertion occurs by a double tendon in the *tuberositas m. tibialis cranialis*.

The *m. extensor digitorum longus* (EDL, Figs 1e, 4a and 5a) lies deep on the cranial surface of the tibiotarsus, beneath the TC, with a fleshy origin between the *crista cnemialis cranialis* and the *lateralis* and along the proximal third of the craniomedial aspect of the TBT. The tendon of insertion passes through the fibrous *pons supratendineus*, crosses the intertarsal joint and is under

the ossified *retinaculum extensorium*. The tendon of insertion sends three branches to digits II, III and IV.

The m. gastrocnemius (G, Figs 1c,d and 2a,b) is a large muscle and the most superficial of the caudal aspect of the TBT. The pars lateralis [G(1)] arises by a flat and thick tendon on the *tuberculum m. gastrocnemius lateralis*; the pars intermedia [G(i)] is the smallest one, arising by fleshy fibres and also with a small tendon on the fossa popliteal. In one specimen, an extra head was found with a tendinous and fleshy origin on the medial aspect of the TBT, these two heads fuse together and, and then, this pars fuses with the pars medialis [G(m)]. This pars is the largest one, with a fleshy and tendinous origin on the external facet of the crista cnemialis cranialis. The three parts converge first in an aponeurosis and then form a wide robust tendon that, after going through the tibial cartilage, inserts on the posterior surface of the hypotarsus.

The *m. flexor perforans et perforatus digiti II* (FPPDII, Figs 2a and 4b) has a small tendinous origin below the *tuberculum m. gastroc. lateralis*, a relatively large belly and, as all the *m. flexor perforatus* and *perforans et perforatus* described below, the tendon of insertion crosses the tibial cartilage and the shaft of the TMT, above the tendons of the FDL and FHL. This tendon inserts on the proximo-medial aspect of the second phalanx of digit II. No vinculum was found between this muscle and FPPDIII.

The *m. flexor perforans et perforatus digiti III* (FPPDIII, Figs 1d, 2a and 4b) is located cranial to the FPPDII and is smaller than this muscle. It arises by fleshy fibres on the *caput fibulae* and inserts on the proximal lateral end of the third phalanx of digit III.

The *m. flexor perforatus digiti II* (FPDII, Figs 4b and 5d) has two heads of origin on the lateral aspect of the shaft of the femur and the *fossa poplitea* and an insertion on the proximal lateral end of the first phalanx of digit II.

The *m. flexor perforatus digiti III* (FPDIII, Figs 1d and 4b) is a small muscle with one head of origin and a fleshy origin on the *region intercondyloidea* of the femur also shares a tendon with the FPDIV. It inserts on the proximal–medial end of the second phalanx and is fused with on the sheath that inserts on the first phalanx of digit III.

The *m. flexor perforatus digiti IV* (FPDIV, Figs 4b and 5d) originates by fleshy fibres and with a tendon from the *fossa poplitea*; this tendon is common to the FPDIII. The insertion occurs on the proximal base of the fourth phalanx of digit IV.

The *m. flexor hallucis longus* (FHL, Figs 1d, 4b and 5d) has two heads of origin, a more lateral one that arises above the *tuberculm m. gastrocnemius lateralis* by both a tendon and fleshy. The second head arises from the *fossa*

poplitea by a thin tendon that is located on the most caudal spot of the *fossa poplitea*. These two heads fuse into a fusiform belly that is located above the FDL. The tendon of insertion is robust and flat on the *cartilage tibialis* and along the shaft of the TMT is ossified, fuses with the tendon of the FDL by a strong *vinculum* and finally inserts on the flexor tubercle of the hallux.

The *m. flexor digitorum longus* (FDL, Figs 1f, 4b and 5b,c) is the largest muscle of the TBT, located mostly on the caudal aspect but also on the medial and lateral one. At least three heads are discernible, all with fleshy origins along the edge of the proximal epiphysis and the shaft of the TBT and the shaft. The tendon of insertion is similar to that of the FHL, flat and thick at the *tibial cartilage*, ossified along the shaft of the TMT and linked with the FHL just anterior to the caudal epiphysis; it trifurcates to the four digits and inserts strongly on the *tuberculum flexorium* of the ungual phalanges.

The *m. popliteus* (P, Figs 1f and 5c) is a small muscle located on the proximal part of the caudal aspect of the shaft of the TBT where it originates by fleshy fibres and connects the fibula by a fleshy insertion.

The *m. extensor hallucis longus* (EHL, Fig. 4a) has two heads; the largest one originates by fleshy fibres on the joint capsule from the TBT and the smallest head arises on the anterior medial surface of the proximal epiphysis of the TMT. These two bellies join at the beginning of the tendon of insertion that goes along the shaft of the TMT and inserts on the extensor tubercle of the hallux.

The *m. flexor hallucis brevis* (FHB, Fig. 4b) has one belly that arises by fleshy fibres on the posteromedial facet of the TMT, extending onto the medial side of the hypotarsus. This belly tapers and has a tendon of insertion from the proximal half of the shaft of the TMT. This tendon has two insertions on the medial and lateral side of the proximo-plantar surface of the first phalanx of the hallux.

The *m. abductor digiti II* (AbDII, Fig. 4a) is a short and small muscle in this species and could easily be overlooked; it has a fleshy origin on the anterior medial surface of the distal epiphysis of the TMT and inserts by a small tendon on the medial aspect of phalanx 1 of digit II.

The *m. adductor digiti II* (AdDII, Fig. 4b) is small with a fleshy origin on the posterior proximal aspect of the TMT, on the *sulcus flexorius* beneath all the posterior muscles. The tendon of insertion runs along the shaft and finally inserts on the proximal end of the first phalanx of digit II.

The *m. adductor digiti IV* (AdDIV, Fig. 4a) arises by fleshy fibres on the anterolateral aspect of the TMT on the *sulcus extensorius*. Its belly extends one quarter of the muscle and then a tendon of insertion runs along the

shaft to the proximo-medial side of the first phalanx of digit IV.

The *m. abductor digiti IV* (AbDIV, Fig. 4b) arises by fleshy fibres, on the lateral edge of the *sulcus flexorius* lateral to the hypotarsus. The long tendon of insertion, about three quarters of the muscle, inserts on the lateral surface of the first phalanx of digit IV.

Quantitative data

The mass of the muscles showed that the *m. flexor digitorum longus* was the largest one (4.034g). There were only three muscles with values between 2 and 2.5 g *m. femorotibialis lateralis* and *intermedius*, the *m. tibialis cranialis* and the *m. gastrocnemius*. Finally, the rest of the muscles did not exceed 1.5 g (Table 1).

The masses of the muscles of one hindlimb represented 7.064% of total body mass (Table 1). The muscle masses

of the pelvic, knee and ankle joints represented each about 20% of the total mass of the hindlimb, while the digits accounted the remaining 40%. The pelvic and ankle joints had similar proportions of flexor and extensor masses, whereas the knee joint presented a higher mass of extensors over flexors and the digits had a predominance of flexors over extensors (Fig. 3).

Discussion

The myological pattern of *T. alba* was similar to that of the other studied Strigiformes (Garrod, 1873, 1874; Hudson, 1937; Volkov, 2004). The muscles *m. ambiens*, *m. flexor cruris lateralis*, *m. fibularis longus*, *m. plantaris* were absent, like in the Strigidae studied (Hudson, 1937; George and Berger, 1966; Volkov, 2004). Also, the muscles *m. extensor propius digiti III, m. extensor propius digiti IV* and *m. lumbricalis* (small muscles of the TMT) were

Table 1. List of the muscles found in the hindlimb of *Tyto alba*, with the abbreviation, mean mass (in g), standard deviation (SD) and the main muscle action taken from Mosto (2014)

Muscle	Abr.	Mean	SD	Main muscle action
m. iliotibialis cranialis	IC	0.572	0.048	Hip flexion
m. iliotibialis lateralis	IL	0.923	0.189	Hip flexion and extension of TBT (weak)
m. iliofibularis	IF	1.352	0.286	Flexion of TBT
m. iliofemoralis externus	IFE	0.035	0.049	Femur abdduction
m. iliofemoralis internus	IFI	0.020		Femur abduction and outward rotation
m. iliotrocantericus caudalis	ITC	0.735	0.143	Hip flexion
m. iliotrocantericus cranialis and medialis	ITCr + M	0.207	0.042	Hip flexion
m. flexor cruris medialis	FCM	0.653	0.157	Hip extension and flexion of the TBT
m. ischiofemoralis	ISF	0.343	0.116	Hip extension
m. pubo-ischio-femoralis	PIF	1.177	0.208	Hip extension
m. obturatorius lateralis	OL	0.060	0.014	Femur outward rotation
m. obturatorius medialis	OM	0.134	0.023	Femur outward rotation
m. caudofemoralis	CF	0.045	0.007	Hip extension
m. femorotibialis lateralis and intermedius	FTL	2.337	0.414	Extension of TBT
m. femorotibialis medialis	FTM	0.293	0.040	Extension of TBT
m. fibularis brevis	FB	0.222	0.040	Inward rotation of TMT
m. tibialis cranialis	TC	2.147	0.293	Flexion of TMT
m. extensor digitorum longus	EDL	1.067	0.227	Extension of digits II–IV
m. popliteus	Р	0.085	0.024	
m. gastrocnemius	G	2.188	0.319	Extension of TMT
m. flexor perforans et perforatus digiti II	FPPDII	0.422	0.050	Flexion of digit II
m. flexor perforans et perforatus digiti III	FPPDIII	0.242	0.041	Flexion of digit III
m. flexor perforatus digiti II	FPDII	0.425	0.081	Flexion and adduction of digit II
m. flexor perforatus digiti III	FPDIII	0.372	0.086	Flexion of digit III
m. flexor perforatus digiti IV	FPDIV	0.598	0.098	Flexion of digit IV
m. flexor hallucis longus	FHL	1.463	0.079	Flexion of digits I–IV
m. flexor digitorum longus	FDL	4.034	0.423	Flexion of digit II–IV and aid flexion of digit I
m. extensor hallucis longus	EHL	0.143	0.040	Extension of digit I
m. flexor hallucis brevis	FHB	0.092	0.024	Flexion of digit I
m. abductor digiti II	AbDII	0.080	0.044	Abducction of digit II
m. adductor digiti II	AdDII	0.065	0.078	Adducction of digit II
m. abductor digiti IV	AbDIV	0.070		Abduction of digit IV
m. adductor digiti IV	AdDIV	0.053	0.043	Adducction of digit IV
	Sum	22.652		

not found in *T. alba*, unlike in the Strigidae where they were present (Volkov, 2004).

The main differences between the muscles of *T. alba* and Strigidae might be considered as minor mainly because these differences have to do with the number of heads of origin. For example, one head of origin in the *m. fibularis brevis* in *T. alba* versus two heads in the Strigidae (Volkov, 2004), both heads of origin in the *m. obturatorum lateralis* in *T. alba* and just the ventral head in Strigidae (Volkov, 2004); or the fusion of muscles in *T. alba* like the *m. ilitrochantericus cranialis* and *medius* and *m. femorotibialus lateralis* and *intermedius* whereas in Strigidae are separated (Volkov, 2004).

The percentage of the hindlimb muscle mass in T. alba represented a 14.13% for both limbs with respect to the body mass. This value agrees with that found for T. alba (13.8%) and other Strigidae (Otus choliba (10.64%), Pulsatrix perspicillata (13.6%), Strix nigrolineata (10.96%), Ciccaba virgata centralis (9.86%) and Asio clamator (16.86%); Hartman, 1961). Also, when this value, 14.13%, is compared with that of other species that also rely on their feet for obtaining food, like Falconidae or Accipitridae species, the percentage of the hindlimb muscle mass is within this range of values too, for example Milvago chimango (9.42%, Mosto et al., 2013), Falco sparverius (8.12%; Mosto, 2014), Buteogallus meridionalis (16.67%; Mosto, 2014) and Buteogallus urubitinga (15.4%, Hartman, 1961). With respect to the percentages of flexor and extensor muscles across each joint in T. alba, the flexors of the digits were the muscles with the higher mass. Those muscles are important for seizing and catching prey (Goslow, 1967), so their relatively greater development is expected. This is also a condition found on diurnals birds of prey (e.g. Buteogallus urubitinga, Falco sparverius; Mosto et al., 2013; Mosto, 2014). The main difference between nocturnal and diurnal raptors is appreciated in the m. flexor digitorum longus and m. flexor hallucis longus. The former muscle is more developed than the latter in Strigiformes, while the opposite situation occurs in Falconidae and Acciptitridae. This is related to the disposition of the digits that both groups have zygodactyl and anysodactyl, respectively (Goslow, 1972; Ward et al., 2002).

Our understanding of avian myology has steadily improved over time. However, the qualitative and quantitative aspects of the muscles of several other genera have yet to be studied. Gross features of the hindlimb muscles and individual muscle mass data constitute basic and necessary information. After having acquired this information, the next step is to continue towards a biomechanical and ecomorphological study of *T. alba*'s hindlimb through the analysis of the physiological crosssectional area to estimate forces while grasping (in prep.).

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Conflict of Interest

There are no conflict of interests.

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