Summary

Cytogenetic analysis of the coat-colours-genetics in the Tobacco-mouse

The gene responsible for the typical coat colour of the tobacco mouse can be assigned to one of the acrocentric mouse chromosomes No. 2, 7, 10, 18, 19.

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Anschrift des Verfassers: A. Radbruch, Pathologisches Institut der Universität, 53 Bonn, Universität

Some Behaviour Patterns of the southern Right Whale *Eubalaena australis*

By G. S. Saayman and C. K. Tayler

Museum, Snake Park and Oceanarium Humewood, Port Elizabeth, South Africa

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Introduction

Little is known concerning the social behaviour of the baleen whales and systematic descriptions of even the most fundamental and stereotyped behaviour patterns are lacking. The seasonal appearance of the southern right whale *Eubalaena australis* (Fig. 1) close inshore in sheltered waters off the South African coast from May to November affords opportunities of observing behaviour from elevated coastal vantage points or at close range from boats. It appears that the whales migrate to calve and

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mate in bays along the south-eastern Cape coast, whereafter they move south to reach the Antarctic in late summer and early autumn (Best 1970). Prominent activities such as breaching, showing the flukes above the water, fluke beating, and lying inverted on the surface with flippers extended characterise the behaviour of individuals at this time. Pairs or trios of animals engage in extensive bodily contact, involving caressing and stroking of the partner with flippers and flukes; such interactions have been described as *courtship* and *mating* (Donnelly 1967, 1969).

Fig. 1. An immature southern right whale bull stranded in Algoa Bay, October 1971

Extensive observation of interacting whales reveals that it is extremely difficult to follow individual behavioural sequences through to their conclusion. Even when interacting at the surface, the ponderous animals are barely visible above the waterline. As much of the action initiated at the surface continues when the animals submerge, it is all but impossible to reliably identify individuals in the majority of cases when the whales surface, unless prominent white patches or scars serve as identification marks. However, the presence of white markings on the dorsal surface is apparently rare in both the North Pacific right whale (Omura et al. 1969) and in the southern right whale (Best 1970). Likewise, it is virtually impossible to identify bulls and cows in the absence of distinctive morphological features: although in the North Pacific mature cows are thought to be longer than adult bulls (Omura et al. 1969), this criterion is not applicable under field conditions, particulary as southern right whales often frequent murky river outlets and themselves create further turbidity by stirring up silt from the seabed. Payne and McVay (1971) have outlined similar difficulties in determining the sex of humpback whales *(Megaptera novaeangliae)* at sea. Technical aids are of great value under such conditions of observation, particularly as observers lack continuous close-range observational experience of these 17 m cetaceans comparable to that now available for the smaller odontocetes in oceanaria. The present report presents findings derived mainly from the frame-by-frame analysis of ciné-film obtained of three interacting southern right whales in Algoa Bay, supported by observations made over several years in many of the bays along the south-eastern Cape coast.

Materials and Methods

A group of approximately seven southern right whales was reported at 0900 hrs about 0,8 km offshore in Algoa Bay (34° S 25° E) on September 18th, 1970. At 1230 hrs the group of whales was dispersed over more than 4 sq km and observations commenced on an interacting trio of whales 20 m distant from the motor launch in a water depth of 6—7 fathoms.

Behaviour was filmed with a Minolta 8D 10 ciné-camera equipped with: variable frame speeds, 8—50 frames/sec; intervalometer with shutter intervals of 0,5—60,0 sec; variable exposure time and single frame exposures; and a continuously variable 7—70 mm telephoto zoom lens. Kodakchrome II film was exposed, from which individual frames were examined and black and white prints of relevant behavioural sequences were photographed with a 35 mm still camera directly from the frame being viewed in a modified projector.

A Piezo-electric hydrophone was kept in the water when the boat was stationary and recordings of underwater sounds were obtained on an Akai Mark V taperecorder. A complementary commentary on behavioural interactions was recorded on an additional taperecorder.

In addition, further extensive observations of southern right whales have been obtained from elevated coastal vantage points during concurrent studies of free-ranging dolphins (Tayler and Saayman 1972, Saayman, Tayler and Bower, in press; Saayman, Bower and Tayler 1972; since the observer is frequently able to look directly down upon the animals, such observations are not restricted by the low angle of inclination which hampers observation from boats.

Results

As the observers approached the group of whales, one animal breached in the distance, and filming then commenced. The following account is a sequential analysis of subsequent behaviour. Supplementary observations, obtained on other occasions, are inserted where appropriate.

Breaching: A whale, identified by a notch on one fluke (see Fig. 11), breached seven times in succession. The first leap occurred before the camera was operational, but was similar to the second. On the second breach, the whale left the surface at an angle of 80° to the horizontal, showing both flippers (Fig. 2). It inverted to fall on its back and disappeared completely beneath the surface, throwing up an immense spray of water. The flukes then appeared and were protruded vertically above the surface (Fig. 3); they then moved about 10° from the vertical and disappeared beneath, giving the impression that the whale had performed a complete somersault underwater and that the head was now facing the direction opposite to that from which the approach was made. On the third breach the whale, already partially inverted, appeared at an angle of 70° to the horizontal, fell on its side and again completely disappeared. The flukes then protruded, one higher than the other, indicating that the animal was still on its side. The fourth breach was less spectacular, the head alone appearing 15° to the horizontal before plunging beneath, pushing

Fig. 2 (above) and 3 (below). A whale at the height of its leap, flippers outstretched, inverts to fall on its back. The head plunges beneath and the flukes then appear above the surface. (Photo from ciné-sequence)

before it foaming white water; the flukes did not appear. The fifth breach commenced as did the third, but the flukes protruded symmetrically above the surface and revolved as they disappeared, indicating that the animal had twisted sideways underwater. On the sixth breach, the whale appeared 45° to the horizontal, again on its side, twisting to strike the surface with the throat and lower jaw, the head disappearing as the back arched strongly clear of the surface without the flukes showing. The final breach was similar to the sixth, except that the flukes again showed vertically, moved until they were horizontal to the surface, and then disappeared.

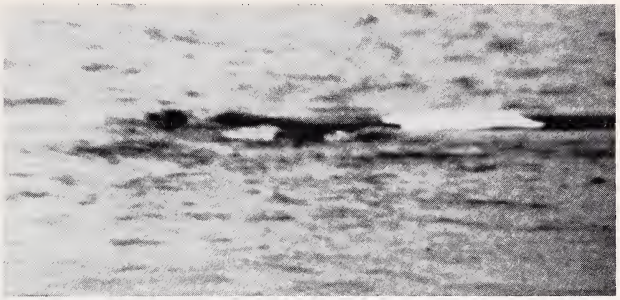

Fig. 4. Two whales lie side by side. The prominent white patch on the dorsal surface served to identify one animal. (Photo from ciné-sequence)

Leaps occurred at irregular intervals, sometimes separated by several minutes, and became progressively less forceful. No animals were seen close to the whale when it commenced breaching, but with each successive leap it progressed in the direction of a pair of interacting whales, which it subsequently joined.

Behavioural Interactions: After the final breach, the whale joined two others which were already interacting. It was possible, during the ensuing engagement of the three animals, to identify a number of behavioural patterns and approaches and, in some cases, to identify individuals by means of prominent white patches on the back of one animal (Fig. 4) and by the notch on the flukes of the whale which breached.

Pushing the partner

The active whale approached at an angle of 90° and, with its lower jaw in contact with the dorsal surface of the passive partner, pushed it sideways (Fig. 5) or some-

Fig. 5. A whale pushes its horizontal partner sideways with its lower jaw in contact with the dorsal surface in the vicinity of the blowhole. (Photo from ciné-sequence)

Fig. 6. A whale rests its lower jaw upon the submerged head of its partner. (Photo from ciné-sequence)

times rolled it completely over. On occasion, this activity ceased with the head of the initiating whale resting on the dorsal surface of the passive partner (Fig. 6). There were many variations, for example, when the initiating animal thrust directly at the flank of the passive partner or when it slid slowly beneath the ventral surface, sometimes inverting as it did so. Further, the angle of approach varied, and contact was established at different points along the axis of the body of the passive whale.

Fig. 7 (above) and 8 (below). Two frames from a ciné-sequence show the final phases of a sweep with the flipper as the active whale moves past the head of its passive partner

Caressing with flipper and flukes

The active whale approached the partner at an angle of 90° but, instead of pushing with the head, turned sideways and stroked the stationary partner from the abdomen to the head with a flipper (Figs. 7, 8). Stroking with the flipper was sometimes followed by a caress with the flukes as the active whale moved alongside to come parallel to the stationary partner.

Presentation of the belly to the partner

The active whale (A) circled in front of the stationary partner (B), in so doing rolling on its side to expose its belly to the head of B. As A righted itself, B then turned on its side to present its belly to the head of A. B then turned upright and A again rolled to present its belly to B for a second time. It was noteworthy that in the first two instances rolling occurred as the genitalia of the presenting whale came opposite the head of the partner.

Adoption of vertical posture

The whale slowly swung the body downwards until, in contrast to the normal horizontal posture, it assumed a vertical position with the bonnet clear of the surface (Fig. 9), sometimes with the mouth slightly ajar. On one occasion, one of a pair of interacting whales adopted the vertical posture and confronted an approaching whale which became stationary and then rapidly withdrew, whereupon the interaction between the original pair of animals recommenced. Although the vertical posture has been observed on numerous occasions, the eyes of the whale have never been seen above the waterline.

Adoption of inverted posture

Interactions were occasionally suspended when one partner rolled upon its back, sometimes with the flippers held vertically (Fig. 10). On other occasions, a similar posture was adopted but the flukes of a second whale were seen to be in contact with the abdomen of the inverted animal.

On November 6th 1971 one of pair of interacting whales in Plettenberg Bay twice lay inverted on the surface with flippers extended and penis erected for approximately two mins in each case following extensive bodily contact between the pair.

Fig. 9. A whale adopts a vertical posture and confronts an approaching individual. The partner of the vertical animal is behind it and submerged. The bonnet of the vertical animal is visible but the eyes of whales in this position were never seen above the surface. (Photo from ciné-sequence)

Subsequent interactions were initiated by the bull which approached from the rear and placed its head beneath the flukes of the partner; in one case the partner responded by rolling to lie inverted belly to belly beneath the bull, one flipper extended upright and held flat against the flank of the bull. The second erection was seen 6,0 mins after the first in an interaction which was observed from 0945 to 1025 hrs.

Fig. 10. An inverted whale lies motionless, holding the flippers clear of the surface. (Photo from ciné-sequence)

The whales were frequently observed to float in the following attitudes: (a) on their sides with their ventral surfaces in close contact and their heads in proximity, (b) one animal lying with its dorsal surface uppermost and the partner inverted beneath it with their heads still in proximity and their ventral surfaces in contact, (c) as in (a) or (b) but with one partner rotated through 180° so that its head was in the proximity of the flukes of the other.

Protrusion of the flukes above the surface

Interactions were occasionally suspended when one of the partners lay motionless at the surface with its flukes protruding and waving slowly in varying attitudes (Fig. 11). This gave the impression that the body was vertical with the head pointing at or resting upon the seabed; this impression was possibly erroneous since this posture has also been seen in water too shallow to accommodate the full length of the animal. On one occasion, whilst in this attitude, the flukes quivered violently before being lowered beneath.

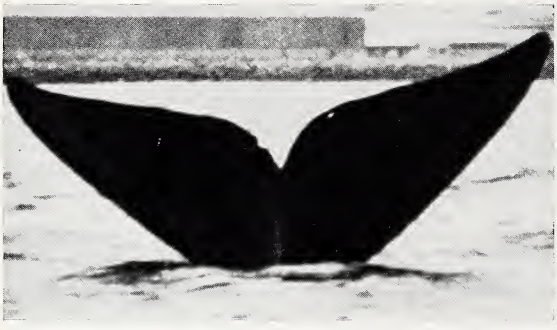

Fig. 11. The flukes of a whale are held clear of the surface and remain motionless in this attitude for a considerable period. This individual was identified by the V-shaped nick in the fluke on the left side and by the hole in the fluke on the right side. (Photo from ciné-sequence)

Striking with the flukes and flippers

One whale slowly lifted its flukes clear of the water and, in so doing, brushed the head of the partner which was lying directly in line behind it. After a pause, it then brought its flukes sharply down, striking the water above the head of the partner.

On October 14th, 1970, a single whale in Plettenberg Bay beat its flukes on the surface: the animal protuded the flukes and part of the peduncle and then brought the flukes down sharply four times in rapid succession. After lifting the head to breathe, the whale again struck the surface with its flukes eight times in the same

manner, throwing up a great amount of water. It then swam rapidly away and disappeared from view out to sea. On the previous day two trios of interacting whales had been observed in the area, and interacting whales were again seen on the two days following this incident. On October 16th, four whales were observed interacting in a single group. One of these animals gave 15 successive strokes with its flukes in the direction of the other whales interacting 10 m away. The flukes then disappeared and the whale surfaced inverted, with both flippers held vertically. After a pause, it rolled sideways and struck the water forcibly with a flipper. Shortly after this the group broke up into two pairs, each of which continued to engage in stroking, pushing and carressing behaviour.

Waving the flippers and striking the surface was seen when a whale was fully or partially inverted with one or both flippers above the surface. Undoubtedly some striking with the flipper occurred as a whale rolled sideways, but a variety of flipper movements occurred during active interactions and included forceful and apparently deliberate striking similar to fluke beating.

Reversal of Behavioural Roles

Intensive examination of filmed sequences and comparison of the roles adopted by individuals in different interactions indicated that oppositely sexed partners possibly performed similar behavioural roles. Thus, it was clearly established that the whale identified by white patches on its dorsal surface adopted both the active and the passive roles in pushing and caressing sequences: at times the animal lay passive whilst being pushed and caressed, whereas in further sequences it actively approached to push and caress the passive partner. In addition, the white-backed whale was temporarily inactive following the arrival of the notch-fluked whale and interactions occurred between the newcomer and the unmarked animal. Thus extensive interactions occurred between the unmarked whale and the two identifiable individuals. It was further established that the notch-fluked whale struck the white-backed whale on the head with its flukes.

The white-backed whale at one time was photographed in an inverted position with its genitals above the surface and several frames were exposed as it rolled towards the camera. Two small slits, resembling the mammaries, were apparent on either side of the genital slit, suggesting that this whale was a cow: positive sexing of this animal, however, was questionable in view of the long-range photography and the graininess of the colour film.

Further reversal of behavioural roles was apparent when two whales alternately presented their bellies to each other as described above in the relevant section.

Phonation

No underwater sounds attributable to the whales were recorded. However, a single bellow, similar in pitch, timbre and intensity to that of domestic cattle, was heard when two of the trio of whales were interacting on the surface. The third whale which at that time was detached from the interacting pair, turned immediately and swam towards them. It was thought that this airbourne sound, undetected by the hydrophone, must have emanated from the blowhole which, in all three animals, was at the time above the surface of the water.

Responses to the Boat

The whales in general gave no indication of being aware of the presence of the boat. Indeed, as the observers approached the trio of whales, a lone individual surfaced

to breathe within 4 m of the boat. In contrast to this apparently inadvertent close approach by a whale, one of the interacting trio emerged a body length away and abeam of the stationary vessel whilst filming was in progress. The animal dived under the boat, and narrowly avoided scraping the keel before the motors could be started. This direct approach was interpreted as an unmistakable challenge, and filming was then carried out at a greater distance without further incedent.

Location of interacting whales

Interactions between whales frequently continued throughout the day in a variety of locations in the comparatively sheltered waters of bays. The whales apparently allowed themselves to be carried by tidal and surface currents. Drifting occurred whether the animals were interacting or, on occasion, lying motionless side by side for more than an hour, during which time they drifted approximately one km. However, when interacting whales found themselves on the fringe of the breaking waves of the surf zone they rapidly made for deeper water before recommencing interactions.

Discussion

The manner of copulation in whales has long been a matter of speculation by cetologists (Slijper 1962, 1966). Indeed, until the observation of an erection by a bull in a pair of interacting whales in Plettenberg Bay, there was no firm evidence that any of the behaviour described in this report comprised part of the copulatory pattern. Nevertheless, the function of many of the interactions and postures described is still open to speculation and, failing underwater observation or photography from close range in good visibility, only an extremely opportune sighting will permit the determination of the postures adopted during coitus and the duration of the consummatory responses.

The question of the behavioural roles adopted by bulls and cows is also a contentious one. It was clear from the present analysis that one individual might adopt both the active and the passive roles in similar behavioural encounters and it therefore seems unjustified at this stage to postulate that the most active animal in an interacting pair or trio of whales must necessarily be a bull (see Donnelly 1967, 1969). This consideration is further reinforced by the great difficulty experienced in obtaining reliable quantitative data upon which to base a conclusion. Furthermore, positive sexing of a whale when it inverted and clearly displayed its genitalia to the observer was, in our experience, a rare event and, even when this did occur, as in the example sited at Plettenberg Bay, continuous identification of that whale during subsequent interactions generally became impossible. In many terrestrial species the sexual partners interchange behavioural roles during the sequences comprising the full pattern of copulatory behaviour. For example, the jackal *Canis aureus syriacus* performs a series of actions prior to copulation, including a characteristic T-sequence: one jackal circles to stand perpendicular to the other and may rest its head briefly upon the back of the horizontally positioned partner. The behavioural roles are interchangable in relation both to the sex and to the body position of the partners. In other words, both partners may alternatively perform identical behavioural responses and, although individual differences between pairs are apparent, the female is in some cases more active and may even vigorously mount the male and perform thrusting movements (Golani and Mendelssohn 1971). Similarly, quantitative studies of captive bottlenosed dolphins *(Tursiops aduncus)* indicate that typical postures and forms of display swimming and leaping, which are characteristic of courtship sequen-

ces, occur with equal frequency in oppositely sexed partners; in free-ranging dolphins as many as ten animals may participate in courtship sequences and on occasion four bulls, all displaying erections, have attempted to mate simultaneously with a single partner (Saayman, Tayler and Bower, in press). More recent experience in the Port Elizabeth Oceanarium has shown that adult bulls attempt insertion with other adult or immature bulls and further, an immature bull, displaying the full clasping and thrusting pattern, may attempt intromission with the most dominant adult bull in the colony. This behaviour occurs despite the presence of a sexually mature cow and its three year old female calf and interactions frequently alternate between like sexed and oppositely sexed partners. Clasping and thrusting behaviour may also occur between two mature cows which sometimes exhibit similar interactions with an adult bull partner. Homosexual behaviour between two captive *Tursiops truncatus* cows has also been reported to alternate with heterosexual interactions (Brown, Caldwell and Caldwell 1966) and McBride and Kritzler (1951) record attempts by young *Tursiops truncatus* to copulate with older dolphins of either sex. In the Amazon dolphin *(Inia geoffrensis),* homosexual interactions occurred between an adult and an immature bull kept together in captivity (Layne and Caldwell 1964) and Tavolga (1966) describes extensive homosexual contacts between immature bull bottlenose dolphins. Whereas conditions of captivity may very well elicit atypical behaviour, the large groups of free-ranging dolphins, sometimes including calves, which we have observed to engage in courtship-like behaviour, suggest that such interactions may well form part of the normal behavioural repertoire of these cetaceans. The details and functions of such behaviour in delphinids (*Tursiops* and *Sousa* sp.) are as yet unclear but it is possible that these social interactions may operate not only in the context of primary sexual behaviour but also as a form of "greetings" ceremony when groups of dolphins come together after having been widely dispersed over the feeding grounds along the coastal stretches over which they range.

In the interactions between the trio of whales which formed the primary basis of this report, it was impossible to arrive at a satisfactory resolution of the likely sex of the partners. There were several possible combinations, assuming that all of the animals were sexually mature, whereas an additional possibility is that one animal might have been a calf or juvenile, in which case interactions similar to those described as "mating" might well form part of the normal interactions between a cow and its immature offspring. It is clear that our present state of knowledge permits little more than a rigorous description of behavioural events as they are seen to occur: any statements concerning the complete behavioural patterns involved in coitus, the sex of the interacting animals and the functions of the postures adopted are premature and, at best, highly speculative.

Summary

The seasonal appearance of southern right whales *(Eubalaena australis)* off the South African coast from May to November provides opportunities to observe the behaviour of interacting pairs or trios of whales from boats or coastal vantage points.

This report describes a number of typical behavioural sequences derived primarily from the frame-by-frame analysis of a cinematographic record obtained from a boat of three interacting whales in Algoa Bay.

Characteristic behavioural sequences of individuals include leaping, fluke beating, lying inverted on the surface with flippers extended and the adoption of a vertical posture with the bonnet visible above the surface. Pairs or trios of whales engage in sequences in which the active partner pushes and caresses the passive partner. A variety of inverted postures are adopted by individuals during behavioural encounters.

Identification of two individuals by means of white patches on the dorsal surface of one whale and by a notch on the fluke of another indicated that whales alternately adopted similar active and passive behavioural roles: a whale might on occasion lie passive whilst

being pushed and caressed, whereas in subsequent sequences it adopted the active role. This finding suggests that it is unjustified to assume that the active whale in an interacting pair is necessarily a bull.

A comprehensive description of behavioural units is not yet possible, but the evidence suggests that much of the behaviour observed comprises part of the copulatory pattern of behaviour.

No underwater sounds attributable to the whales were recorded. However, an airbourne bellow is described.

Zusammenfassung

Einige Verhaltensweisen der Südlichen Glattwale

Das jahreszeitliche Erscheinen der Südlichen Glattwale *(Eubalaena australis)* an der südafrikanischen Küste von Mai bis November bietet die Gelegenheit, das Verhalten von Paaren oder Trios der Wale zu beobachten, und zwar von Schiffen oder von Beobachtungspunkten entlang der Küste.

Dieser Bericht beschreibt eine Reihe typischer Verhaltenssequenzen von drei miteinander agierenden Walen in der Algoa Bay. Die Ergebnisse werden durch eine Analyse von Filmen gewonnen, die von einem Boot aus aufgenommen wurden.

Die charakteristischen Verhaltensweisen schließen ein: Springen, Schwanzschlagen, umgekehrt auf der Oberfläche liegen mit ausgebreiteten Flossen, vertikale Position mit über dem Wasserspiegel sichtbarer Kappe. Die Walpaare oder Trios engagieren sich in Sequenzen, bei denen der aktive Partner den passiven stößt oder liebkost. Während des Zusammentreffens werden von den einzelnen Partnern verschiedene Positionen eingenommen. Zwei Wale konnten durch weiße Rückenflecke und durch eine Kerbe am Schwanz identifiziert werden, dadurch wurde erkannt, daß die Tiere abwechselnd die aktive oder passive Rolle übernehmen.

So blieb ein Wal passiv liegen, während er gestoßen und liebkost wurde, während er später die aktive Rolle übernahm. Diese Beobachtung läßt darauf schließen, daß es falsch ist anzunehmen, daß der aktive Wal ein Bulle sein muß. Eine umfassende Beschreibung ist noch nicht möglich, aber alle Beweise deuten darauf hin, daß vieles von dem beobachteten Verhalten mit der Paarung in Zusammenhang steht.

Unterwassergeräusche der Wale wurden nicht festgestellt, jedoch wird ein in der Luft ausgestoßener Schrei beschrieben.

Acknowledgements

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Authors' address: G. S. Saayman and C. K. Tayler, Museum, Snake Park and Oceanarium Humewood, Port Elizabeth, South Africa

Artenzahl und Publikationen — Untersuchungen zur Säugetierliteratur

Von Hans-Reiner Simon

Aus dem Zoologischen Institut — Bibliothek — der Universität Heidelberg

Eingang des Ms. 29. 6. 1972

1. Einleitung und Fragestellung

Die Entstehung der biologischen Literatur sowie ihre Verteilung auf systematische Einheiten und Ursprungsländer ist von verschiedenen Parametern abhängig. Sie werden von Rothman und Woodhead (1971) sowie von Solla-Price (1971) diskutiert. Zu nennen sind besonders Forschungsmittel, Anzahl beteiligter Wissenschaftler sowie sozialer Typus des Landes, in dem die Forschungen angestellt werden. Da all diese Parameter jedoch nur schwer oder überhaupt nicht beschaffbar sind, beschränkt man sich meist auf die Erfassung der Publikationen, um damit eine Situationsanalyse von Forschungsbereichen durchzuführen. Auf diese Weise gewinnen wir variable Größen, welche es gestatten, Verteilungsmuster der biologischen Literatur innerhalb bestimmter systematischer Einheiten (z. B. Stämme, Ordnungen) darzustellen (Simon 1971). Als Vergleichswert, der möglichst auch Interpretationswert besitzt, ist jedoch neben der Publikationszahl eine zweite Variable erforderlich. Sie wurde in Form der Artenzahl pro Ordnung bereits bei einer allgemeinen Analyse der biologischen Literatur, jedoch ohne statistische Absicherung, eingesetzt (vgl. Simon 1971, p. 124). Dabei zeigte sich, daß bei relativ großen Artenzahlen auch entsprechend hohe Publikationsanteile auftraten. Diese Feststellung gilt innerhalb des gesamten Tierreiches, mit Ausnahme der Säugetiere. Hier wurde vielmehr deutlich, daß bei relativ niedriger Artenzahl der Mammalia im Vergleich zum übrigen Tierreich eine Zunahme von Publikationen zu verzeichnen war. Diese Abweichung soll nachfolgend im einzelnen überprüft und die auch für die Säugetierliteratur vermuteten Korrelationen zwischen Artenzahl und Publikationsanteil statistisch bestimmt werden.

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