Lung Morphology of Cursorial and Non-Cursorial Mammals: Lagomorphs As a Case Study for a Pneumatic Stabilization Hypothesis

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ABSTRACT Gross lung morphology is examined in representative species from four genera within the order Lagomorpha (Lepus californicus, Sylvilagus nuttalli, Oryctolagus cuniculus, Ochotona princeps), and compared with a representative rodent out-group (Spermophilus richardonsii). Examination of pulmonary morphology reveals several correlations between the thoracic morphology and locomotor behavior. Lepus, the most cursorial species, exhibits a distinct suite of characteristics: 1) tissue of the right cranial lobe interposed between the heart and sternum; 2) well-defined grooves in the lung tissue for both the aorta and ribs; 3) a fibrous pericardial attachment to the sternum; 4) relatively large heart and lung mass. Sylvilagus, a sprinter, exhibits these features to a lesser degree, whereas Oryctolagus and Ochotona, non-cursorial species, lack most of these features. This same suite of pulmonary features is also observed in a wide range of unrelated cursorial taxa (including selected Artiodactyla, Perissodactyla, Carnivora). Corrosion casts of the internal airways demonstrate that the cursorial and non-cursorial taxa examined here have similar branching patterns despite their variable external morphologies. The juxtaposition of pulmonary lobes, heart, and ribs leads to the hypothesis that the lungs themselves provide mechanical support of the heart and visceral mass during locomotion. Analyses of cineradiographic and pneumotachographic data obtained from Oryctolagus tend to support a pneumatic stabilization hypothesis: the lungs themselves, intimately associated with the chest walls and positively pressurized during landing, may provide some mechanical support to the viscera. This mechanism may be important in stabilizing the relatively large hearts of the most cursorial species during running.

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The order Lagomorpha is well suited for examining the relationship between gross lung morphology and locomotion. Within this small but behaviorally diverse monophyletic clade, closely related species exhibit a wide range of body size and locomotive ability. Lagomorphs include two families, Ochotonidae (pikas) and Leporidae (rabbits, cottontails, and hares). Ochotonidae is considered to be the more primitive family and is composed of non-cursorial species (Gambaryan, '74; Dawson, '81; Corbet, '83). The leporids include numerous species whose cursorial specializations have been well documented (Camp and Borell, '37; Howell, '65; Gambaryan, '74; Schnurr and Thomas, '84; Bramble, '89b). Hares (Lepus) are the most specialized runners, combining speed, endurance, and agility (Howell, '65; Gambaryan, '74; Bramble, '89b).

This study examines gross pulmonary morphology primarily within the order Lagomorpha. The objectives are three-fold: 1) to describe the lung morphology and the relationships of the lung to adjacent thoracic elements (ribs and heart) of selected cursors and non-cursors, 2) to experimentally evaluate the functional implications of pulmonary design using data from high speed cineradiography and pneumotachography from domestic rabbits, and 3) to introduce an hypothesis of a non-respiratory function for mammalian lungs. Based on morphological and behavioral differences, particular attention is given to contrasts between the functional lung morphology of the endurance runner Lepus californicus and the similarly sized but less cursorial Oryctolagus cuniculus. Lung morphology of representative species from the orders Rodentia, Artiodactyla, Carnivora, and Perissodactyla are also included for comparison.

MATERIALS AND METHODS
Phylogenetic considerations

Gross lung morphology, airway branching patterns, and locomotor behaviors were examined in representative lagomorph species from four genera: Lepus californicus (n = 15), Sylvilagus nuttalli (n = 8), Oryctolagus cuniculus (n = 25), and Ochotona princeps (n = 10) (Fig. 1). Observations from Lepus townsendii (n = 4) are also included as the pulmonary morphology of L. townsendii is indistinguishable from that of L. californicus. Rodentia is widely considered to be the sister group to Lagomorpha (Novacek and Wyss, '86). A non-cursorial rodent species, Spermophilus richardsonii (n = 7), representing the most primitive rodent suborder Sciurognathi (Nowak, '91), was included for out-group comparison and character polarization. Unfortunately, the phylogenetic relationships among the leporids remain largely unresolved (Dawson, '81; Corbet, '83). For the purposes of this study, the phylogenetic hypothesis from Hibbard ('63; Fig. 1) is used, but other phylogenetic hypotheses (Corbet, '83; Biju-Duval et al., '91) would not substantially change the conclusions of this study. In addition to lagomorphs and rodents, cursorial and non-cursorial species from the orders Artiodactyla (i.e., pronghorn antelope and domestic pigs) and Carnivora (i.e., dogs, cats, and raccoons) are considered in this study.

<table>
<thead>
<tr>
<th>Species</th>
<th>Body mass g</th>
<th>Behavior</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spermophilus richardsonii</td>
<td>262 - 504</td>
<td>Sprinter (non-cursorial)</td>
</tr>
<tr>
<td>(ground squirrel)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ochotona princeps</td>
<td>113 - 202</td>
<td>Sprinter (non-cursorial)</td>
</tr>
<tr>
<td>(pika)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lepus californicus</td>
<td>1300 - 3100</td>
<td>Endurance runner (highly cursorial)</td>
</tr>
<tr>
<td>(black tailed jack rabbit)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sylvilagus nuttalli</td>
<td>628 - 1300</td>
<td>Sprinter (moderately cursorial)</td>
</tr>
<tr>
<td>(desert cottontail)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oryctolagus cuniculus</td>
<td>1350 - 3004</td>
<td>Sprinter/Digger (non-cursorial)</td>
</tr>
<tr>
<td>(European rabbit)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 1. Phylogenetic relationships (Hibbard, '63), body mass, and characteristic locomotor behavior of species examined. 1. From Chapman ('75), Burt and Grossenheider ('80), Lim ('87), Smith and Weston ('90). 2. From Nowak ('91).
**Morphology**

All but one lagomorph species examined were collected from their natural habitats (collection permits obtained from Utah Division of Wildlife Resources and Nevada Department of Wildlife); Oryctolagus, the domestic rabbit, was obtained from a laboratory colony at the University of Utah. Morphological observations and measurements were made on freshly dead specimens. Dried lungs were prepared by washing excised lungs with water to remove blood, then inflating the lungs of fresh, hydrated lungs to greater than 100% total lung capacity (to compensate for shrinkage; see below) with an air source at the trachea and allowed to dry (Hildebrand, '68). As an estimate of the contact area between lungs and chest wall, projected surface area measurements were obtained from video images of the dry lungs using NIH-Image software. Images were acquired with a Panasonic camera (AG-450) and VCR (AG-7390) interfaced with a Power Macintosh computer. No lateral measurements were made of Ochotona’s left lung; some distortion of the specimens precluded reliable measures. However, in life, and before air-drying) the right and left lungs of Ochotona are symmetrical. Therefore, the surface area measures from the right lung are sufficient to describe both the right and left lungs.

As air-dried lungs dehydrate, some shrinkage occurs (Murphy and Engel, '80). Whole lung shrinkage and regional lobar distortion were calculated by comparing the dimensions of dried lungs to fresh, hydrated lungs. Data from tests using Oryctolagus lungs demonstrated that whole lung shrinkage in lateral projection was approximately 20% ± 2.3% of projected surface area, and the shrinkage of individual lobes was not significantly different from that of the whole lung (Table 1).

**TABLE 1. Comparison of projected surface areas of hydrated vs. air dried lungs in adult Oryctolagus cuniculus**

<table>
<thead>
<tr>
<th>Lung Tissue</th>
<th>% Shrinkage (std err)²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole lung</td>
<td>20.33 (2.30)</td>
</tr>
<tr>
<td>Cranial lobe</td>
<td>18.65 (2.17)</td>
</tr>
<tr>
<td>Middle lobe</td>
<td>26.68 (3.92)</td>
</tr>
<tr>
<td>Caudal lobe</td>
<td>18.34 (4.09)</td>
</tr>
</tbody>
</table>

¹All data based on lateral view of right lungs. N = 5.
²Cranial, middle, and caudal lobe shrinkages are not statistically different from that of the whole lung. (one-way ANOVA; p = 0.332).

To further characterize gross lung morphology, the primary branching patterns of the pulmonary airways were examined using corrosion casting techniques. Dow Corning silicone rubber (base #3112 and catalyst 1; ratio 20:1) was injected into the airways of lungs that were retained within the isolated (i.e., decapitated, limbs removed) but unopened thorax. The thorax was maintained in a “standing” posture. The lungs were removed from the thorax following a twenty-four hour curing period and lung tissue was dissolved using a concentrated NaOH solution. The corrosion casts confirmed the accuracy of the gross morphology of the *in vitro* dried lung preparations.

For comparative purposes, dried lungs from other representative mammalian species (e.g., pronghorn antelope, raccoon, pig, and dog) were prepared in the same manner described above. Additional information on the pulmonary anatomy of various domestic species (e.g., dogs, cats, and pigs) was obtained from the literature (Getty, '75; Evans, '93).

**Kinematic and pneumotachographic data**

Oryctolagus (n = 3) were trained over a four-month period to run on a variable speed treadmill. Clear, plexiglass walls prevent individuals from dodging laterally or leaping off the treadmill. At all but the fastest running speeds, leporids use a half-bound. This asymmetrical gait is similar to a gallop in that the forelimbs contact the ground sequentially. However, both the right and left hind limbs move almost in synchrony throughout the stride cycle. Cineradiographic films (100 fps) were taken of two rabbits during unencumbered treadmill exercise using facilities available at Harvard University (Bramble and Jenkins, '93). Films were analyzed using a Vanguard Motion Analyzer (Vanguard Instrument Corp., Melville, NY). The positions of the 8th thoracic vertebra, the 3rd sternebra, the heart, and the liver, were all digitized for sequences of film in which the animals were running steadily at speeds of 8–16 kph. Both forelimbs were visible in the radiographic films and thus enabled forelimb placement to be documented. Oryctolagus is a burst runner, running for approximately 15–45 seconds continuously. The segments of film in which the rabbits were perfectly positioned in front of the x-ray tube (i.e., entire thoracic compartment plus anterior edge of visceral mass visible) comprise a random sample of running.

Upon return to the University of Utah, all three rabbits were trained to wear a face
mask fitted with a screen pneumotachograph (nylon screen mesh 36% open; 7 mm radius). An Omega differential pressure transducer (0–7 inches H2O) was mounted on the face mask, and air flow at the mouth was recorded while the animal was running. Combined weight of the mask and the transducer was 35 grams. The pneumotachograph signal (sampled at 300Hz) was synchronized with a simultaneous video recording of locomotion and recorded using a Macintosh computer and custom designed software. A pulse of light (LED) was simultaneously visible on the video tape and recorded electronically along with the pneumotachograph recording. Video kinematics of the trunk, forelimbs, hind limbs, and head were analyzed using a Peak Performance System.

Radiodensity analysis (Bramble and Jenkins, '93) was used to determine the phases of the respiratory cycle in the cineradiographic films for which no pneumotachographic data were available. In subsequent cineradiographic and pneumotachographic experiments, synchronized kinematic and respiratory data from these rabbits confirmed the regular relationship between the pneumotachographic, limb support, and radiodensity patterns (unpublished data).

RESULTS

External morphology of the pulmonary lobes

There are striking differences in the shape and relative size of pulmonary lobes among lagomorphs. The lungs of three leporids (Lepus townsendii, Oryctolagus cuniculus, and Sylvilagus nuttalli) are illustrated in Figures 2, 3. Terminology identifying lung lobes, consistent with the Nomina Anatomica Veterinaria ('94), will be used throughout this paper. The four lobar descriptors: cranial, middle, caudal, and accessory, are equivalent to the terms: apical or anterior; cardiac; diaphragmatic or posterior; and intermediate, respectively. All three leporid species have six lobes: right and left cranial lobe, right and left caudal, right middle, and right accessory lobe. However, in contrast to the externally symmetrical disposition of the right and left cranial lobes observed in Oryctolagus, both Sylvilagus and Lepus show pronounced cranial lobar asymmetry (Fig. 2). In Sylvilagus, the anterior portion of the right cranial lobe turns medially toward the ventral midline. A similar but more exaggerated condition occurs in Lepus; the right cranial lobe completely crosses the sternum to contact the left chest wall. The dorsal, anterior portion of the left cranial lobe of Lepus is relatively reduced in size and thus accommodates the extended wrapped-around right cranial lobe (Fig. 3B). The caudal lobes comprise approximately 50% of the projected surface area in direct contact with the chest walls and the cranial and middle lobes together comprise the remaining 50% (Figs. 3, 4; Table 2).

Ochotonids exhibit symmetry of the right and left lungs and have three distinct lobes in each. In contrast to the leporid condition, the cranial lobes of Ochotona have a relatively greater projected lateral surface area in contact with the chest walls (Table 2). Differences in relative size and geometry of ochotonid and leporid pulmonary lobes are illustrated in Figures 2–4, and Table 2. In contrast to the condition in lagomorphs, examination of the rodent outgroup reveals that the left lung of Spermophilus richardsonii is undivided. S. richardsonii shows no extension of the right cranial lobe. The right lung is divided into four lobes: cranial, middle, caudal, and accessory (Figs. 4B, C, 5B).

The lungs of dogs, horses, pigs, and pronghorn also show varying degrees of right cranial lobe extension resulting in separation of the heart from the anterior chest wall and sternum (Speransky, '62; Getty, '75; pers. obs.). This arrangement is most pronounced in the pronghorn, Antilocapra americana (Figs. 2F, 4D, E), an extremely specialized endurance runner (Howell, '68; Lindstedt et al., '91). As is observed in Lepus, a portion of the right cranial lobe of Antilocapra lies against the left chest wall and comprises approximately 20% of the left lateral projected surface area (Fig. 4E). A pronghorn’s right cranial lobe has its greatest anteroposterior thickness directly anterior to the heart. Domestic pig lungs show a very similar external morphology, but the wrap-around portion of the right cranial lobe is relatively smaller than that of the pronghorn. Although less pronounced than the pulmonary anatomy of the hare or pronghorn, the lungs of dogs also exhibit an enlargement of the right cranial lobe such that there is a thickening of lung tissue directly anterior to the heart (Getty, '75; Evans, '93; pers. obs.). Horse lungs are alobate but nonetheless show a cranial extension of the right anterior region of the lung ( Getty, '75). In contrast, such non-cursors as raccoons, primates, bats, and geomyid rodents possess an external pul-
Fig. 2. Anterior views of air-dried lungs. A: Lepus townsendii. B: Ochotona princeps. C: Sylvilagus nuttalli. D: Spermophilus richardsonii. E: Oryctolagus cuniculus. F: Antilocapra americana (new born). Lobar identification: A, cranial; L, left; M, middle; P, caudal; R, right. Cardiac fossa (f) is created by RA, RM, LA, and LM for all species except (D) S. richardsonii, in which the right accessory (X) lobe also participates. Scale bar = 1 cm. Note: Lungs of L. californicus and L. townsendii are morphologically indistinguishable. Both species of jack rabbit are behaviorally similar and have over-lapping ranges of body mass.
Fig. 3. Lateral views of air-dried leporid lungs. **A, B**: *Lepus townsendii*. **C, D**: *Sylvilagus nuttalli*. **E, F**: *Oryctolagus cuniculus*. Notice grooves on *L. townsendii* and *S. nuttalli*, where lobes are in contact with ribs of lateral chest walls. See legend of Figure 2.

monary morphology (pers. obs.) similar to that of the ground squirrel in having relative symmetry of the right and left cranial regions of the lung.

The accessory lobe branches off the right bronchus, posterior to the middle lobe, and is visible only in caudal view (Fig. 5A, B). This lobe lies caudal to the heart and separates the heart and diaphragm. The morphology of the accessory lobe of *Lepus townsendii* (Fig. 5A) is representative of the lagomorph condition and is also superficially similar to that of *Spermophilus richardsonii* (Fig. 5B). Despite the similar general shape and orientation of the accessory lobes among all lagomorphs, the projected caudal surface area of the accessory lobe, measured as a percentage of the total projected caudal surface area, varies among species. The accessory lobe accounts for 25.8% (+1.5 standard error) of the surface area in *Lepus* (n = 3), whereas in *Oryctolagus* (n = 3), it comprises only 15.5% (+0.3). *Sylvilagus* (n = 3) and *Ochotona* (n = 3) have indistinguishable surface areas of 18.7% (+1.1) and 18.9% (+1.2), respectively. Among the lagomorphs, the relative
 Laguna LUNG MORPHOLOGY

Fig. 4. Lateral views of air-dried lungs from out-group taxa. A: Ochotona princeps. B, C: Spermophilus richardsonii. D, E: Antilocapra americana. RA', right cranial lobe against left chest wall. See Figure 2 legend.

caudal surface area varies positively with relative heart mass (see Table 3 below). Spermophilus richardsonii (n = 5) has the largest relative accessory surface area at 30.3% (±1.7) of the total projected caudal surface area. This relatively large percentage in S. richardsonii may be explained by the observation that a portion of the right accessory lobe is in contact with the left chest wall (Fig. 5B) and that the position of the accessory lobe in this rodent is analogous to that of both the accessory lobe and the ventral portion of the left anterior lobe in leporids (Fig. 4C).

In all species examined, the heart and great vessels are surrounded by lung tissue. The cranial, middle, and accessory lobes form a well-defined pocket or cardiac fossa surrounding the heart (Figs. 2, 4, 5). This fossa encom-
TABLE 2. Projected surface areas of pulmonary lobes of selected lagomorphs as a percent of total lateral projected area

<table>
<thead>
<tr>
<th>Lobe</th>
<th>Ochotona princeps</th>
<th>Oryctolagus cuniculus</th>
<th>Sylvilagus nuttalli</th>
<th>Lepus californicus</th>
</tr>
</thead>
<tbody>
<tr>
<td>LA¹</td>
<td>—</td>
<td>42.62 (3.29)</td>
<td>44.45 (2.70)</td>
<td>45.67 (1.18)</td>
</tr>
<tr>
<td>LP</td>
<td>—</td>
<td>57.38 (3.29)</td>
<td>55.55 (2.70)</td>
<td>46.62 (1.23)</td>
</tr>
<tr>
<td>RA²</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>7.71 (0.31)</td>
</tr>
<tr>
<td>RA</td>
<td>76.35 (2.34)</td>
<td>32.52 (2.69)</td>
<td>33.77 (2.43)</td>
<td>36.90 (1.37)</td>
</tr>
<tr>
<td>RM</td>
<td>13.78 (1.93)</td>
<td>21.38 (1.86)</td>
<td>20.59 (2.24)</td>
<td>25.03 (3.35)</td>
</tr>
<tr>
<td>RP</td>
<td>9.87 (0.82)</td>
<td>46.10 (3.10)</td>
<td>45.65 (3.59)</td>
<td>38.07 (2.02)</td>
</tr>
</tbody>
</table>

¹LA, left cranial; LP, left caudal; RA, right cranial against left chest wall; RM, right cranial; RP, right caudal. n = 4 per genus. Standard error in parentheses.
²No measurements from Ochotona princeps left side (see text).

Table 2 shows the projected surface areas of pulmonary lobes of selected lagomorphs as a percent of total lateral projected area. The data is presented in a table format with lobes and corresponding percentages for each species.

passes the heart almost completely in Lepus and to a lesser degree in Sylvilagus, Oryctolagus, and Ochotona. In Spermophilus richardsonii, the cardiac fossa is created by the left lung together with the right cranial, middle, and accessory lobes (Fig. 2D).

To varying degrees, lung structure also reflects interactions with the primary intrathoracic vasculature. The thoracic aorta passes through a deep and clearly defined sulcus in the left lung. This groove maintains its structural integrity when the lungs are excised and dried in the absence of the aorta. All lagomorph species possess such an aortic groove, although it is slightly less pronounced in Oryctolagus and Sylvilagus than in Lepus and Ochotona. Antilocapra also shows a well-defined groove. No groove is visible in Spermophilus richardsonii. In all specimens, portions of the accessory lobe and right caudal lobe form a tunnel through which the caudal vena cava passes just before reaching the heart. The esophagus traverses a smaller opening also created by the accessory lobe, right caudal lobe, and to a lesser extent, the left caudal lobe (Fig. 5).

Airway branching patterns

Although the external morphology of the lungs reveals obvious lobar structural differences among species, the internal branching patterns of the major airways, as evidenced by corrosion casts, are similar among these species. In all species examined, the right lung has a primary bronchial pattern that includes an anterior branch, a middle branch, and a posterior branch (Fig. 6). The left lung has an anterior branch and a posterior branch, but only the ochotonid shows a left middle branch (Fig. 6B). The internal branch-

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**Fig. 5.** Caudal view of air-dried lungs. **A:** Lepus townsendii, representative of all lagomorphs. **B:** Spermophilus richardsonii. e, channel for the esophagus; M, middle portion of the left cranial lobe; RP, right caudal lobe; v, opening for the vena cava; X, accessory lobe. Dorsal surface is up.
The branching pattern of Spermophilus richardsonii (Fig. 6A) is very similar to that of the leporids, although there is no external lobation of its left lung. Branching patterns of dogs (Woldenhiwot and Horsfield, '78) and pigs (Speransky, '62) are also similar to those of rodents and rabbits (Fig. 6E, F). However, despite these similar internal branching patterns, both pigs and dogs exhibit an externally distinct, left middle lobe.

**Integration of lungs and ribs**

Comparisons of *in situ* and excised lung tissue reveal that the lungs maintain their
form (i.e., grooves, borders) following inflation and air-drying. The external structure of the lung is defined by the endoskeleton of the lung itself. This fibrous skeleton of interwoven collagen and elastin fibers (Weibel, '84), combined with the integrity of the pleural membrane, results in gross anatomical features that maintain their identity when the lungs are excised. Thus, surface topography of the lungs reflects, but is not solely dependent on, the lung’s juxtaposition with thoracic structures.

The series of sulci and tori (grooves and ridges) on the lateral lung surface indicate that lobes of the lung have an intimate and interlocking relationship with the adjacent ribs and chest wall (Figs. 2, 3). All 12 ribs in leporid species are associated with grooves and ridges on the lung surface. The grooves are pronounced in Lepus, less well defined in Sylvilagus, and poorly expressed in Oryctolagus. Rib-grooves are weakly developed in Ochotona, and Spermophilus richardsonii, has no apparent grooves. Interspecific differences in the depth of the costal grooves are independent of the inflation volumes used while preparing the lungs (see Materials and Methods).

Pericardial morphology

In Lepus, the heart is attached firmly to the sternum via the sternopericardial ligament—a fibrous portion of the pericardial sac. This ligament anchors the apex of the ventricles to the third sternebra. The two-layered (fibrous and serous) pericardial sac is attached to the sternum in a similar location in all leporid species. However, in Lepus, the pericardium is tough and opaque due to a high fibrous component of the sac, whereas in Oryctolagus, it is extremely thin and transparent due to a lower fibrous content. Sylvilagus shows an intermediate condition with a relatively small fibrous contribution to the pericardium. In Ochotona and Spermophilus richardsonii, the dominant component to the pericardial sac is serous, and thus neither species shares the fibrous anchoring of the heart observed in Lepus.

Relative mass of lungs and heart

The scaling relationships of mammalian heart and lung mass were examined using Crile and Quiring’s ('40) large data set, which includes 100 species, 71 genera, and 12 orders of mammals. The slopes for heart and lung mass relative to body mass are not significantly different from 1.0 (Stahl, '65; Prothero, '76). Average lagomorph data from the present study fall within the expected mammalian pattern of relative heart and lung mass when mapped onto the larger data set (Fig. 7). However, a comparison of heart mass among lagomorph genera with different locomotor behaviors reveals that the endurance runner, Lepus, has a relative heart mass approximately 2–4 times larger than that of the non-endurance runners, Oryctolagus, Sylvilagus, and Ochotona (Table 3). The lung masses of Lepus, Ochotona, and Spermophilus richardsonii are those predicted by the general mammalian scaling relationship of isometry, but the lungs of Oryctolagus and Sylvilagus are relatively smaller than those predicted for their body mass (Fig. 8). As with heart mass, comparisons within the order Lagomorpha reveal that Lepus has a relative lung mass considerably larger than that of Oryctolagus, Sylvilagus, and Ochotona (Table 3). Unfortunately, no wild Oryctolagus specimens were available for examination in order to assess a possible influence of domestication on the size of the heart and lungs. However, such comparative measurements of the heart are available from the literature (Hesse, '21). These data show no significant differences (Student t-test; \( p < 0.05 \); \( n = 7 \) in each category) in heart mass between wild and domestic Oryctolagus. In addition, Hesse's ('21) values for the heart mass of domestic Oryctolagus are not significantly different (\( p = 0.40 \)) from those measured in this study.

The difference in heart and lung size between Lepus and the other lagomorph species suggests that endurance runners, generally, might have relatively larger hearts and lungs. To test this prediction, the residuals of heart and lung mass were calculated for species from 28 terrestrial mammalian families and plotted for two groups of cursorial mammals classified according to locomotor behavior: 1) endurance runners and 2) sprinters (Fig. 8). Locomotor behavior is relatively uniform within a family (with the notable exception of Leporidae) and hence this taxonomic level was selected for analysis. The following group classifications are modified from Van Valkanberg ('85): 1) endurance runners: specialized for sustained, aerobic running, > 500 meters (e.g., antelopes, wolves, and jack rabbits); 2) sprinters: short-distance runners, < 500 m, short bursts of speed (e.g., ambush hunters as well as animals that sprint to
Fig. 7. Interordinal scaling relationships of log heart mass (top) and log lung mass (bottom) against log body mass (Crile and Quiring, '40). Data from Crile and Quiring ('40) (squares) from which regression is calculated; Lagomorpha shown with open circle. Heart mass slope = 0.99 ± 0.02; Lung mass slope = 1.02 ± 0.02.

safety such as mountain lions and cotton-tails, respectively). Residuals for heart mass of endurance runners are significantly above those for sprinters (p < .05). The differences in the residuals for lung mass of the two behavioral groups follow the same trend but are only marginally significant (p = .085) (Fig. 8). These data suggest that mammalian heart and lung mass are correlated with locomotor behavior: endurance runners have relatively larger hearts and lungs than species specialized for sprinting. Again, it is worth emphasizing the range of relative heart masses witnessed within leporid lagomorphs; the difference between *Lepus* and *Oryctolagus* exceeds that of all other families combined (Fig. 8).

**Kinematic and pneumotachographic data**

Kinematic displacements of a half-bounding rabbit (12 kph) are plotted for three representative strides (Fig. 9). The relative positions of the heart, liver, and sternum (with reference to the vertebral column) are superimposed on the simultaneous limb position and respiratory phase. As the first forelimb reaches the ground, the sternum, liver and heart move caudally simultaneously while the vertebral column continues forward until halfway through the forelimb support phase. Although the heart, liver, and sternum undergo simultaneous displacements, it is important to note that, in *Oryctolagus*, neither the heart nor the liver is connected to the sternum (or to one another) by any struc-
TABLE 3. Body, heart, and lung masses of lagomorph species

<table>
<thead>
<tr>
<th>Species (n)</th>
<th>Body mass (g)</th>
<th>Heart mass (g)</th>
<th>Heart/Body %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lepus californicus (14)</td>
<td>2145.21 (90.32)</td>
<td>21.27 (0.94)</td>
<td>0.99 (0.03)</td>
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<tr>
<td>Sylvilagus nuttalli (7)</td>
<td>783.71 (54.55)</td>
<td>2.54 (0.47)</td>
<td>0.32 (0.01)</td>
</tr>
<tr>
<td>Oryctolagus cuniculus (20)</td>
<td>2564.05 (128.59)</td>
<td>6.56 (0.41)</td>
<td>0.26 (0.01)</td>
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<tr>
<td>Ochotona princeps (6)</td>
<td>152.33 (13.64)</td>
<td>0.67 (0.08)</td>
<td>0.44 (0.04)</td>
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</table>

<table>
<thead>
<tr>
<th>Species (n)</th>
<th>Body mass (g)</th>
<th>Lung mass (g)</th>
<th>Lung/Body %</th>
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<tbody>
<tr>
<td>Lepus californicus (5)</td>
<td>1901.00 (106.56)</td>
<td>26.83 (1.64)</td>
<td>1.43 (0.11)</td>
</tr>
<tr>
<td>Sylvilagus nuttalli (4)</td>
<td>781.50 (90.48)</td>
<td>5.76 (0.92)</td>
<td>0.73 (0.08)</td>
</tr>
<tr>
<td>Oryctolagus cuniculus (9)</td>
<td>2238.67 (53.93)</td>
<td>12.81 (0.75)</td>
<td>0.58 (0.04)</td>
</tr>
<tr>
<td>Ochotona princeps (3)</td>
<td>167.33 (17.33)</td>
<td>1.5 (0.04)</td>
<td>0.97 (0.09)</td>
</tr>
</tbody>
</table>

1Standard error in parentheses.
2Lung mass measured from a subset of specimens used for heart measurements.

The current pneumotachographic recordings, together with previous observations (Bramble and Carrier, '83), indicate that, in general, a running rabbit expires during the forelimb support phase and inspires while the forelimbs are off the ground (Fig. 9). The phase relationships were determined by analyzing the synchronized video and pneumotachographic data. Respiratory volumes were then estimated in the cineradiographic sequences from a radiodensity analysis of the films (see Materials and Methods). The pooled pneumotachographic data from three individuals show a characteristic locomotor-breathing coupling ratio of 1:1 approximately 55% of the time (i.e., 40 of 73 stride cycles). The remaining 45% of the time, the rabbits showed either an alternative ratio of 1:2 or no locomotor-respiratory coupling.

**DISCUSSION**

**Comparative morphology**

The results of this study reveal several correlations between the thoracic morphology and locomotor behavior of four lagomorph species. *Lepus*, the most cursorial species, exhibits a distinct suite of characteristics: 1) tissue of the right cranial pulmonary lobe interposed between the heart and sternum; 2) well-defined grooves in the lung tissue for both the aorta and ribs; 3) a strong, fibrous pericardial attachment to the sternum; and 4) relatively large heart and lung mass. *Sylvilagus*, a sprinter, exhibits these features to a lesser degree, whereas *Oryctolagus* and *Ochotona*, both non-cursorial species, lack most of these features entirely. These apparent correlative patterns between morphology and behavior are corroborated by additional morphological and physiological data from several previous studies on lagomorphs. Gross muscular and skeletal differences among *Ochotona*, *Lepus*, and *Sylvilagus* (Camp and Borell, '37) parallel a morphocline of locomotor specialization in which *Ochotona*, the least cursorial, represents one extreme and *Lepus*, the most cursorial, represents the other (Hall and Kelson, '59). The dominant fiber type of the locomotor musculature differs significantly between *Lepus* and *Sylvilagus*. The muscles of hares (*Lepus*) have a much greater oxidative capacity than those of cottontails (*Sylvilagus*), which reflects the endurance running capabilities of *Lepus* versus the sprinting behavior of *Sylvilagus* (Schnurr and Thomas, '84).

The genera *Lepus* and *Oryctolagus* illustrate two extremes of leporid behavior. In some species of *Lepus*, running jumps may subject the thorax to very large decelerational forces upon forelimb impact (i.e., > 12 g's; Bramble, '89b). Based on their locomotor behaviors, neither *Oryctolagus* nor *Sylvilagus* is likely to experience such large impulsive loads. In its natural habitat, *Oryctolagus* burrows extensively and relies on brief sprints to find shelter from predators (Grzimek, '75). *Sylvilagus* behavior appears to be "intermediate" and includes sprinting and hiding from predators in holes but rarely does it dig the holes itself (Nowak, '91). The present data suggest a morphological gradient that parallels this behavioral gradient.

Interspecific comparisons within North American *Lepus* revealed that, although the body mass of the species examined (*L. townsendii, L. californicus, L. americanus*) varied threefold, the gross lung structure was invariant. This finding, together with the differences in lung structure between...
LAGOMORPH LUNG MORPHOLOGY

Fig. 9. Cineradiographic kinematic data from *Oryctolagus* running steadily (12 kph) on a treadmill. Horizontal displacements of the heart, liver, sternum, and trunk (vertebra) are plotted for three and one half stride cycles (1 second). Horizontal bars indicate when the right (R) and left (L) forelimbs are in contact with the belt. Positions of the sternum, liver, and heart are relative to the vertebral column; note that all three move rearward together in a closely synchronized manner. Scale bars = 1 cm. Breathing cycles are based on corresponding radiodensity profiles of posterior lobes of lungs (see Materials and Methods; Bramble and Jenkins, '93), corroborated by synchronized pneumotachographic and video recordings. Dashed and solid lines demarcate bounds of inspiratory (I) and expiratory (E) flow.

*Lepus* and *Oryctolagus* makes it clear that lung geometry is not a size-dependent phenomenon within the leporids but appears instead to be strongly correlated with locomotor behavior.

Comparative analysis of the external pulmonary morphology within the order Lagomorpha suggests that the inflected right cranial lobe (the wrapped-around portion) of *Lepus* and *Sylvilagus* is a derived condition relative to the out-groups *Ochotona* and *Spermophilus richardsonii*. The presumed primitive condition is also found in geomyid and heteromyid rodents. The evidence from lagomorphs thus suggests that the degree of inflection of the right cranial lobe is positively correlated with endurance running. This raises the question: Does this morphological-locomotor correlation exist among other taxa? Within the order Carnivora, a comparison of right cranial lung morphology among several species appears to correlate with locomotor habit: dogs (endurance runners; Van Valkenberg, '85) show some thickening of the right cranial lobe, whereas cats (sprinters; Van Valkenberg, '85) and raccoons (non-cursors; Howell, '65), show no such elaboration of the right cranial lobe. In addition, there has been the apparent independent acquisition of an extended right cranial lobe in several species of endurance runners within the orders Artiodactyla and Perissodactyla (Getty, '75). This evidence, taken together with the absence of this pulmonary specialization in representative, nonendurance runners from the orders Chiroptera, Rodentia, and Primata (pers.
thus separating the heart from the dia-

Heart. Superficially, the gross morphologies

of the accessory lobe of both Spermophilus

richardsonii and the representative lago-
morph are similar in caudal view (Fig. 5). But
closer examination reveals that different lobes
have produced similar structures. Such a con-
vergent morphological pattern wherein the
heart is surrounded by lung tissue argues
that the lobar structure may have some func-
tional significance related to heart-lung inter-
action (see below).

Airway branching patterns

Evidence presented in this study shows
that divergent external pulmonary lobe mor-
phologies are associated with more conserva-
tive bronchial pathways (Fig. 6). The bron-
chial branching patterns of leporids and the
rodent out-group are more similar to one
another than they are to that of Ochotona.
Ochotona, although considered the primitive
sister taxon of leporids, is a highly specialized
animal. The locomotor behavior of the North
American species, O. princeps, includes
bounding up and down rocky slopes at high
altitude. It is possible that this unusual be-
behavioral ecology may be reflected in its unique
pulmonary structure. However, for the mo-
ment, such an inference is purely speculative
because no Eurasian ochotonid species were
available for comparison with O. princeps.
The similarity of the branching patterns of
leporids and rodents to those of canids and
suids supports the hypothesis that, overall,
mammalian pulmonary branching patterns are
conserved. Data presented here demon-
strate that the external divisions and relative
sizes of the pulmonary lobes are variable by
comparison. Although the branching pat-
terns and airway diameters are important to
airflow patterns in resting animals (Horsfield
et al., '71; Snyder and Jaeger, '83; Tsuda et
al., '90), the functional implications of these
branching patterns in exercising mammals are
little known (but see Bramble and Jen-
kins, '93).

Integrated thoracic unit

The anatomical proximity of lungs, heart,
and ribs implies that these structures may
function as an integrated mechanical unit
during mammalian locomotion. That the
heart, lungs, and ribs are intimately associ-
ated is evidenced by the pronounced cardiac
fossa as well as the distinct costal and aortic
grooves present on the lungs (Figs. 2, 3).
Likewise, the attachment of the pericardial
sac to the ventral chest wall must help main-
tain the heart’s position within the thoracic
cavity, which, in turn, influences the poten-
tial mechanical interaction of the lungs and
heart (Lloyd, '89; Hoffman, '93). In addition,
the residuals of heart and lung mass are
positively correlated indicating that for mam-
mals in general and endurance runners in
particular, the sizes of lungs and heart co-
very (Fig. 8). This offers further evidence
that the various anatomical elements of the
mammalian thoracic complex constitute an
integrated unit.

The location of the lobar divisions may
greatly influence thoraco-pulmonary mechan-
ics. Both the right and left lungs show an
abutting interface between the caudal lobes
and the two cranial lobes (Figs. 3, 10). This
simple contact zone may allow sliding be-
tween the anterior (i.e., cranial and middle)
and caudal lobes. In contrast, the division
between the cranial and middle lobes is such
that sliding between these lobes may be mini-
mized: the cranial and middle lobes overlap
obliquely in the right lung and are almost
entirely fused in the left lung (Fig. 10). The
nature of this lobar junction in the right
lung, and the absence of an articulation in
the left lung suggests that the cranial and
middle lobes together may resist forelimb
loads as a single unit during such times as
the overlying shoulder girdle transmits the
ground reaction forces to the adjacent chest
wall (see Bramble and Jenkins, '93). The
caudal lobes may similarly experience loads
originating from the abdominal muscles and
adjacent visceral mass. A likely source of
such loading would be oscillations of the vis-
ceral mass, thought to be associated with
galloping (Bramble and Carrier, '83; Bramble,
'89b).

Pneumatic stabilization hypothesis

The inflected right cranial lobe, interposed
between the heart and sternum, constitutes
only a small percentage of the total lung
mass (approximately 1.5% dry mass in Lepus
californicus). Seemingly, a symmetrical ex-
tension of the right and left anterior lobes
could produce an equal amount of lung tis-
tue. Thus, there seems to be no simple physi-
Fig. 10. Schematic representation of the right (A) and left (B) lateral views of leporid lungs. Ribs 1–6 overlie the anterior and middle lobes (shaded). These ribs directly join the sternum via short costal cartilages. Ribs 7–12 overlie the posterior lobes (unshaded) and are attached to the sternum via longer costal cartilages that articulate only with the posterior-most sternebra. The dashed line (a–b) indicates the axis along which the anterior and posterior lobes abut. The line (c–d) represents the axis along which the anterior and middle lobes overlap (A) or are externally fused (B). The posterior lobes are loaded directly by the abdominal viscera during abdominal compression.

A

Right caudal

Right cranial

Left cranial

Left caudal

Diaphragmatic surface

B

a

b

c

d

ological (i.e., gas exchange) explanation for the asymmetrical distribution of lung tissue within the cranial lobes of the various species described here. An alternative explanation for this peculiar geometry is mechanical and nonrespiratory: the extended right cranial lobe may act as an air cushion to stabilize and protect the relatively large heart of cursors. In theory, the wrapped-around lobe provides a seamless glove into which the heart could decelerate.

But is there a need for pneumatic stabilization of the heart? Kinematic profiles of running jack rabbits (*Lepus californicus*) point unambiguously to an answer in the affirmative. The thoracic trunk of these hares experiences substantial decelerations on every stride cycle, frequently punctuated by impulsive decelerational loads with magnitudes greater than 10g’s (Bramble, '89b). Trunk dynamics of this type will tend to induce forward inertial displacements of all loosely anchored internal organs, including the heart. For any given trunk deceleration, the force required to check the forward surge of the heart will be directly proportional to its mass ($F = ma$). This is true for both endurance running and sprinting. However, any mechanism employed by *Lepus* to stabilize its relatively large cardiac mass against inertial displacement should be exaggerated in its expression compared to that of leporids with relatively smaller heart masses (e.g., *Oryctolagus* and *Sylvilagus*). Consistent with this idea is the observation that the pronghorn (*Antilocapra*) exhibits a strongly modified right cranial lobe (Figs. 2, 4) coincident with a relatively large heart mass (Fig. 8). It is also worth noting that this inflected and extended right cranial lobe is present at birth in both *Lepus* and *Antilocapra*. In both genera the young are precocial and initiate running behavior at a very early age.

Sharp vertical and horizontal decelerations of the trunk in jack rabbits and domestic rabbits, as well as in other galloping mammals occur over the first half of the forelimb stance phase of the stride cycle (Alexander, '77). It is during this interval that a putative pneumatic stabilizer might act to reduce the impact load on the heart by prolonging the duration of its deceleration and/or by providing a mechanical cushion between the heart and neighboring skeletal structures with which the heart might collide. Chief among these structures are the anterior ribs and sternum, positioned immediately anterior and ventral to the cardiac mass. The threat of collision will be amplified if the impact loading of the forelimbs tends to drive these skeletal elements rearward at the same moment inertial forces are propelling the heart forward.

In order for the lungs to function as pneumatic stabilizers of the heart (or any other visceral mass) in a galloping mammal, the lungs must contain adequate quantities of gas at the time the forelimbs impact the ground. This condition will automatically be met if the ventilation of the lungs is synchronized with that of the locomotor cycle at the appropriate phase angle. Indeed, a 1:1 cou-
pling of gait and breathing cycles has been widely documented in galloping mammals of varying body size and taxonomic affinity (Bramble and Carrier, '83; Bramble, '89b; Young et al., '92a). These data reveal that, in all cases, the onset of the expiratory phase of the breathing cycle is closely coordinated with forelimb impact; expiratory flow from the lungs continues past the point of maximum trunk deceleration. The timing of the expiratory phase is critical to the pneumatic stabilization model in that pulmonary tissue will be most effective as a shock absorber when stiffened by positive internal pressurization. These rapid, forceful expiratory bursts witnessed in galloping mammals, including leporids (Oryctolagus Fig. 9; Lepus californicus Bramble and Carrier, '83), together with the timing of the bursts relative to the forelimb loading cycle, would appear to satisfy the mechanical requirements of a pneumatic stabilization device.

Cineradiographic kinematic data obtained from Oryctolagus running on a treadmill allow an analysis of trunk, sternum, heart, and liver motion during exercise. The data reveal that the vertebral column shears cranially over the sternum while the liver, heart, and sternum all move caudally together during forelimb loading (Fig. 9). As the limb impacts the treadmill, ground reaction forces are transmitted from the limbs to the chest walls via the muscular linkages offered by the pectoralis and serratus anterior muscles. If governed solely by inertial forces, synchronous displacements of the liver, heart, and sternum would be unexpected because the viscera are only loosely connected to the sternum, and the liver out-weighs the heart by one and a half orders of magnitude (i.e., heart mass = 5.2 ± 0.4 g; liver mass = 77 ± 5 g; n = 15). The co-oscillations of the liver and heart, together with their relationship to sternal motion, strongly suggest that the ground reaction force is transmitted from the chest wall to the viscera through the stiffened, positively pressurized lungs. It appears that the relatively light heart, surrounded by lung tissue, is swept rearward, whereas the heavier liver may be pushed caudally by the pressurized lung tissue during expiration and landing.

A model has been constructed based on these data (Fig. 11): the thoracic cage is simplified showing two ribs, the vertebral column and sternum. Ground reaction forces will tend to collapse the thorax by changing its shape from a rectangle to a rhomboid. The lungs provide a mechanical link between the skeletal framework and the otherwise loosely connected viscera. Such a potential, pulmonary-based “stabilizing” link is in contrast with the idea that viscera may move simply, and inertially, inside the thorax during locomotion (Bramble and Carrier, '83; Bramble, '89a).

Pneumatic stabilization of the heart, in summary, requires that the cranial, middle, and accessory lobes wrap around the heart, and that all lobes are intimately fitted against the chest walls. Under appropriately timed positive pressurization within the locomotor...
cycle (i.e., during limb loading and expiration), the stiffened cranial and middle lobes may provide mechanical stabilization of the heart. In species such as Lepus and some artiodactyls, the sternopericardial ligament may also contribute to cardiac positional stability, as there is a mechanical link between the pericardium and the sternum as well as between the heart and vertebral column via the great vessels (i.e., “pericardial restraint”; Lloyd, '89, p. 310).

The degree to which a mammal requires pneumatic stabilization should be reflected in the gross pulmonary morphology and the detailed relationships of the lungs to the adjacent thoracic structures, particularly the heart and chest walls. Although such a mechanism is expected to be more conspicuously developed among highly cursorial mammals (e.g., the extended right apical lobe), it is likely to occur to a lesser degree in all mammals. The cineradiographic data from Oryctolagus reinforce this idea because, even in this non-cursorial lagomorph, there is good evidence of mechanical load transfer between the forelimbs and internal organs (heart and liver) via the intervening lungs. It is probable that the relatively small hearts of sprinters are more easily stabilized pneumatically by the lungs without recourse to the special modifications of the cranial lobes observed in Lepus, Antilocapra, and other strong cursorians. Even though gross morphological differences among species may be striking, all mammals possess lungs at least partially surrounding the heart (Fig. 2). In this sense, the lungs of mammals are positioned to offer some degree of pneumatic support to the heart even in the absence of an overtly inhaled right cranial lobe.

Summary

This study has revealed important variation in lung morphology in lagomorphs that correlates with differences in locomotor behavior. It provides structural evidence to suggest that elements of the thorax (e.g., lungs, heart, ribs) should be considered a functional unit and that differences in pulmonary anatomy are usefully evaluated in the context of locomotor behavior and ecology. The morphological and experimental data presented support a pneumatic stabilization hypothesis that predicts that pulmonary morphology, especially that of the right cranial lobe, may reflect nonrespiratory, mechanical functions associated with pneumatic, cardiac support during locomotion.

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LITERATURE CITED
